Tansley review

Water release through plant roots: new insights into its consequences at the plant and ecosystem level

Author for correspondence:
Iván Prieto
Tel: +33 4 67 61 33 40
Email: ivan.prieto@cefe.cnrs.fr

Iván Prieto, Cristina Armas and Francisco I. Pugnaire

Estación Experimental de Zonas Áridas – Consejo Superior de Investigaciones Científicas (EEZA-CSIC), Carretera de Sacramento

s/n, E-04120 La Cañada de San Urbano, Almería, Spain

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Summary

Hydraulic redistribution (HR) is the passive movement of water between different soil parts via plant root systems, driven by water potential gradients in the soil–plant interface. New data suggest that HR is a heterogeneous and patchy process. In this review we examine the main biophysical and environmental factors controlling HR and its main implications at the plant, community and ecosystem levels. Experimental evidence and the use of novel modelling approaches suggest that HR may have important implications at the community scale, affecting net primary productivity as well as water and vegetation dynamics. Globally, HR may influence hydrological and biogeochemical cycles and, ultimately, climate.

I. Introduction

Water relations are key to understanding the ecology of terrestrial plant communities, and one of the components that determines water balance is the process of hydraulic redistribution (HR; 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 transpiration and other plant processes through water provision to upper roots and its redistribution within the root system. Water efflux from roots in glasshouse experiments was first described in the 1930s (see Ryel, 2004; Caldwell *et al.*, 1998 for a historical perspective) but it was not until 1987 that Richards & Caldwell (1987) coined the term 'hydraulic lift' to describe the upward movement of water from

deep wet to shallow dry soil layers. Water may also move downwards (inverse hydraulic redistribution; Burgess *et al.*, 1998) or laterally (Smart *et al.*, 2005) depending on where dry and moist soil layers are located in the soil profile (Fig. 1). All these processes were termed HR (Burgess *et al.*, 1998).

Hydraulic redistribution is a passive process driven by water potential gradients between soil layers as far as these are connected by an intact root system (Leffler *et al.*, 2005). During the daytime, water is drawn up as plant transpiration forces water inflow from the soil through the stem and out to the atmosphere via stomata. When stomata are closed and transpiration is very low or suppressed at night (for all species except plants with crassulacean acid metabolism), plant water potential equilibrates with that of the soil where most active roots are found, which can
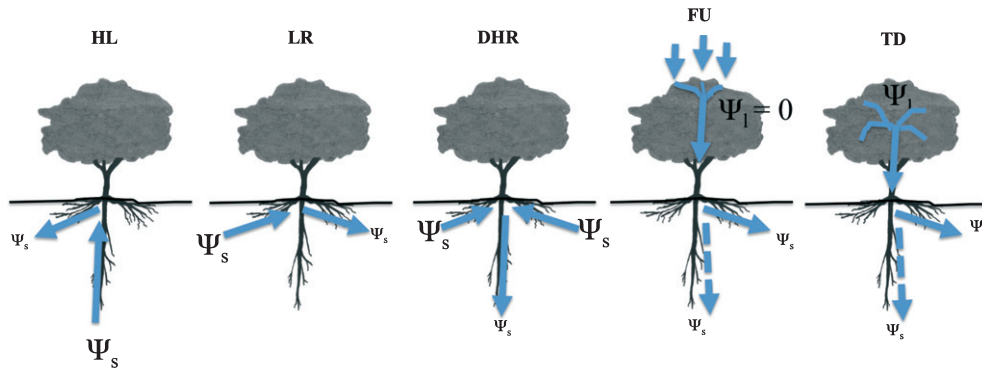
Fig. 1 Scheme of different types of hydraulic redistribution (HR). Hydraulic lift (HL) is the most commonly observed type of HR and takes place when shallow soil layers are drier than deep layers. Lateral redistribution (LR) is the horizontal redistribution of soil water between soil layers at the same depth but with different water potentials. It may occur naturally (Bleby *et al.*, 2010) or be triggered by localized irrigation (Smart *et al.*, 2005). Downward HR (DHR) refers to water movement to deep soil layers under certain conditions when shallow layers are wetter than deep layers (i.e. after a rain event). HR of fog water (FU) occurs when fog events combine with dry soil conditions, and fog water may be taken up by leaves and transferred downwards to the roots and then to the surrounding soil (Burgess & Dawson, 2004; Nadezhdina *et al.*, 2010). Tissue dehydration (TD) is the most extreme type of water movement, occurring at the end of long droughts when both shallow and deep soil layers are very dry and become competing sinks for water stored in above-ground plant tissues (Nadezhdina *et al.*, 2010). Ψ denotes soil or plant water potentials. Different Ψ sizes indicate different water potential (the bigger the symbol, the higher the water potential, i.e. the greater the moisture). Arrows indicate the direction of water movement and dashed arrows indicate alternative pathways for water movement to deep soil layers if drier than shallow soils. Adapted from Nadezhdina *et al.* (2010).
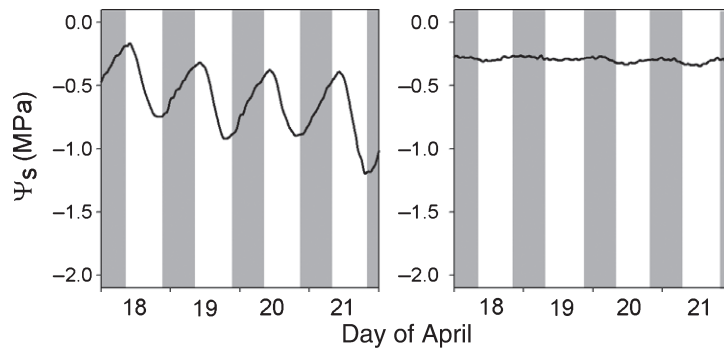

Fig. 2 Daily patterns of soil water potential under *Retama sphaerocarpa* shrubs at 30 cm depicting typical hydraulic lift (HL) cycles (left) and in root-free soil in gaps between shrubs (right). During the day, water flows from the soil to the atmosphere following the transpiration stream, decreasing soil water potential (white bars). At night, water moves from deep to shallow soil layers through the roots. In shallow layers water flows from roots to soil, increasing the soil water potential (gray bars). These cycles do not appear in root-free soil (I. Prieto *et al.*, unpublished data).

result in water potential gradients between the plant and the drier soil points; hence, water flows from roots to these dry soil layers (Fig. 2). Daytime stomatal closure has also been reported for some species under very high vapour pressure deficit (VPD) conditions when radiation is high. Under such conditions, HR can also take place (Espeleta *et al.*, 2004).

The HR process seems to be ubiquitous among plants (Caldwell *et al.*, 1998) as long as conditions favour its occurrence. In some biomes, such as nonsaline wetlands, where soil moisture is high and rather uniform, or prairies where roots may not reach deep enough for plants to reach soil layers with different moisture, HR may not occur. However, only in a very few cases was HR not detected (Huang, 1999; Wan *et al.*, 2000; Scholz *et al.*, 2008; Espino & Schenk, 2009; Grigg *et al.*, 2010); among other reasons this was because it becomes technically difficult to evidence (Caldwell *et al.*, 1998) and serious experimental work is needed to demonstrate that, whenever conditions are favourable for HR, the process does not occur.

Hydraulic redistribution can be detected through a variety of techniques (Table 1) but these are often based on detecting daily fluctuations in bulk soil moisture around roots (Fig. 2). However, these techniques require appropriate controls in root-free soil and time-consuming calibrations to quantify the influence that temperature or other soil processes have on soil moisture (i.e. liquid and vapour water transport) (Katul & Siqueira, 2010; Warren *et al.*, 2011). Alternative methods that do not require the use of such controls include direct measurements of xylem water movement in the root system (Brooks *et al.*, 2002; Bleby *et al.*, 2010) or the use of enriched water isotopes (^{2}H and ^{18}O) applied locally to roots or soil and monitored in other parts of the root system and soil around roots engaged in HR (Dawson *et al.*, 2002). A more detailed description of these methods can be found in Ryel (2004). The most recent techniques include the use of radiography and radioactive isotopes (^{3}H) but their cost and associated difficulties have largely restricted their use (Hawkins *et al.*, 2009; Carminati *et al.*, 2010; Moradi *et al.*, 2011).

Table 1 Main techniques used to measure hydraulic redistribution in both field and glasshouse conditions

Type of technique	Technique	Variable measured		References
Soil moisture	Soil psychrometers	Water potential (Ψ)	Nondestructive	Brown & Bartos (1982); Richards & Caldwell (1987)
	Time domain reflectometry	Water content (θ)	Nondestructive	Topp *et al.* (1996); Wan *et al.* (2000)
	Frequency Domain Capacitance	Water content (θ)	Nondestructive	Paltineanu & Starr (1997); Brooks *et al.* (2002)
Sap flow	Heat ratio method	Sap velocity/direction	Semidestructive	Burgess *et al.* (2000, 2001);
	Heat field deformation	Sap velocity/direction	Semidestructive	Nadezhdina *et al.* (1998, 2006)
	Thermal dissipation	Sap velocity/direction*	Nondestructive	Granier (1987); Brooks *et al.* (2002)
Isotopic	Deuterium (^{2}H)	Direction/quantity of water redistributed	Destructive	Dawson (1993); Brooks *et al.* (2002)
	Oxygen (^{18}O)	Direction/quantity of water redistributed	Destructive	Querejeta *et al.* (2007); Lilleskov *et al.* (2009); Armas *et al.* (2010)
Dye	Fluorescence	Direction/velocity	Destructive	Egerton-Warburton *et al.* (2007)
Radioactive	Neutron radiography	Water content (θ)	Nondestructive	Carminati *et al.* (2010); Moradi *et al.* (2011)
	Tritium (^{3}H)		Destructive	Hawkins *et al.* (2009)

References include the original reference for the technique and examples of representative works that first used these techniques in HR studies.
*Modified from original technique (see Brooks *et al.*, 2002).

Although we have a good understanding of the HR process and several reviews have summarized previous findings (Dawson, 1993; Caldwell *et al.*, 1998; Horton & Hart, 1998; Jackson *et al.*, 2000; Ryel, 2004), research over the past 10 yr has yielded a wealth of knowledge on different aspects of this process. These recent data have shifted our attention on HR from an ecophysiological curiosity to an ecologically significant process ranging from molecular to global scales.

II. Mechanisms controlling HR

1. Competing sinks

Water movement in unsaturated soil layers depends on both soil water potential and gravity, but when gravity is no longer operating, water potentials (matric and osmotic) are the main force for water movement and act as drivers for HR. However, recent experimental evidence indicates that HR is much more complex than previously thought and a complex source–sink system in the plant–soil interface also influences the process (Scholz *et al.*, 2002, 2008). A network of water potential gradients acting as source–sink can be established within the plant as well as between the plant and the surrounding soil, changing HR patterns and magnitude (Scholz *et al.*, 2002; Nadezhdina *et al.*, 2010). Water moves within this network following water potential gradients that depend on soil conditions (i.e. soil moisture), plant physiological status (water relations and differences in water potentials of a variety of tissue/plant organs), and environmental conditions (VPD) (Scholz *et al.*, 2002). This may be the case with night-time transpiration, a common process in species able to redistribute water (Dawson *et al.*, 2007), which may alter competitive sinks for hydraulically redistributed water. Night-time transpiration reduces leaf water potential and forces water up to the canopy, reducing flow to soil, which at night is negatively related to the difference between soil and leaf water potential (Scholz *et al.*, 2002, 2008; Hultine *et al.*, 2003, 2004; Prieto *et al.*, 2010a). Howard *et al.* (2009) showed that night-time transpiration driven by high VPD effectively decreased HR by up to 73%,

a substantial decrease that could affect total carbon gain by lowering plant transpiration rates (Ryel *et al.*, 2002).

Other processes illustrate the source–sink interactions within the plant that affect HR patterns (Fig. 1) and evidence the complex mechanisms that control HR and its heterogeneous and patchy nature (see Bleby *et al.*, 2010).

2. Root size, morphology, function and mycorrhizas

The bidirectional movement of water in and out of roots may imply that water does not meet differential resistance to flow through nonsuberized roots moving in both directions (a detailed discussion on this issue is given in Caldwell *et al.*, 1998). However, most water exchange occurs in the young and distal portions of the root system (Caldwell *et al.*, 1998), and properties of this area affect HR patterns and water flow differently (Dawson, 1997; Warren *et al.*, 2007; Scholz *et al.*, 2008). There is greater root resistance to water flow from roots to the soil than from soils into roots (Dawson, 1997; Schulte, 2006; Valenzuela-Estrada *et al.*, 2009). Root resistance to water flow through roots may change on a daily basis. A large part of this temporal variation is thought to be a consequence of the activity of water-permeable proteins or aquaporins (Henzler *et al.*, 1999). An up-regulation of aquaporins during the day in *Quercus fusiformis* enhanced deep root hydraulic conductivity, whereas aquaporin activity at night was reduced, decreasing root hydraulic conductivity and water flow (McElrone *et al.*, 2007). This may imply a short-term indirect control on plant water loss in upper soil layers through a decrease in water uptake from deep roots or even a decrease in night-time water outflow from roots to dry soils. However, aquaporins are involved only in one of the three main water pathways from soil to roots, as described by the composite transport model (Steudle, 2000), contributing to only about half of the total root conductivity (Siefritz *et al.*, 2002; McElrone *et al.*, 2007). Moreover, McElrone *et al.* (2007) found that fine root hydraulic conductivities during the night associated with aquaporin activity were greater under field than under laboratory conditions, probably because of a greater demand of water for

HR in the field. Thus, the degree to which, if any, aquaporins can control or contribute to HR processes still remains unknown.

Root architecture, morphological attributes such as root density and spatial distribution, and life history traits also affect HR. HR is usually detected in species with dimorphic root systems, whereas monomorphic species lacking true lateral roots in shallow soils usually do not exhibit HR (Scholz *et al.*, 2008; Grigg *et al.*, 2010). Hydraulic connectivity between roots is also a major factor controlling water redistribution. Water flows from a lateral root in wet soil, axially upwards through the stem and then downwards through the stem to the opposite root in dry soil provided these roots are interconnected through the stem (Burgess & Bleby, 2006; Nadezhdina *et al.*, 2009). Radial flow through the stem interconnecting opposite roots of a tree may thus limit the amount of water that can be redistributed within a single night. In highly modular plants with a high stem physical segmentation this may represent an advantage rather than a drawback, as it would prevent water loss through roots in very dry soil (Espino & Schenk, 2009). Not surprisingly, the degree of modularity in plant species decreases from wet to dry environments (Schenk *et al.*, 2008). Finally, suberization of deep roots (Ryel *et al.*, 2003) and loss or death of fine roots (i.e. by low soil water potentials) can also reduce or stop HR.

Mycorrhizal fungi associated with plant roots often improve plant water relations through increased extension of root growth and increased surface absorption (Allen, 2007; Lehto & Zwiazek, 2011), playing a major role in hydraulic redistribution processes. Under dry soil conditions, water can move from roots to soils via mycorrhizal fungi tips (Querejeta *et al.*, 2003) and may also increase the magnitude of HR. For example, efflux of water into the soil is indeed directly correlated to the abundance and viability of ectomycorrhizal fungi in *Quercus agrifolia* seedlings (Egerton-Warburton *et al.*, 2008). In the same way, mycorrhizal fungi may also increase the rate of downward HR (i.e. after a rain event) through greater water absorption as a result of exploration of greater soil volumes than roots alone, potentially increasing the rate of water recharge to deep soil layers; but whether mycorrhizas play a relevant role in this process still remains unknown.

3. Soil environment

Soil type and condition may also affect HR magnitude and patterns. 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 potentials (Hultine *et al.*, 2004). Similarly, soil texture affects the amount of water that roots can release, with decreasing magnitudes of HR in coarser soil types (Yoder & Nowak, 1999; Aanderud & Richards, 2009; Wang *et al.*, 2009), but the relationship between HR and soil texture is not linear (Prieto *et al.*, 2010b) and may result in soil context-dependent HR patterns.

Two other soil properties that determine HR direction and magnitude are conductivity and salinity. The interstitial osmotic potential (Ψ_o) of soil can determine the rate and direction of water movement within the root system independently of the soil matric potential. Dwarf mangle trees (*Rhizophora mangle*) with

roots connecting soil layers with different salt concentrations were engaged in HR independently of soil matric potential (Hao *et al.*, 2009). Although matric potentials were similar in both layers, water moved upwards following the osmotic potential gradient from lower (higher Ψ_o) to higher salt concentrations (lower Ψ_o). As mangle roots are effective in excluding salt during water uptake, the authors hypothesized that freshwater movement upwards should help reduce the high salinity in shallow layers and allow dwarf mangle to avoid damage caused by high soil salinity.

III. Below-ground processes affected by HR

1. Benefits to roots

Do roots benefit from HR? In general roots have longer vessels, which are more vulnerable to cavitation and hydraulic failure than stems, and therefore have narrower safety margins (Martínez-Vilalta *et al.*, 2002). Hence, although roots may be subjected to less tension than stems during transpiration as predicted by the tension-cohesion theory (Tyree, 1997) through overnight provision of water via HR, plants can avoid drops in root water potential below the level that would cause hydraulic failure, a crucial process to withstand long drought spells (Domec *et al.*, 2004). HR alone may be able to maintain root hydraulic conductivities at safe water potentials (Domec *et al.*, 2006) and often root embolism can recover when HR occurs (Domec *et al.*, 2004). Loss of root conductivity negatively affects both root water transport capacity and leaf stomatal conductance. Thus, reducing plant water stress and maintaining or recovering root conductivity overnight may help to increase stomatal conductances the next day and overall carbon gain, increasing plant fitness (Domec *et al.*, 2006). However, maintaining root conductivity in dry soils may come at the expense of losing more water through HR. Embolism formation and losing part of the root system comprise a mechanism of preventing whole-plant failure and water loss through roots, which improves plant survival under drought conditions (Sperry & Hacke, 2002). Nevertheless, maintenance of active roots in moderately dry soil may improve plant water relations through increased use of transient soil moisture (e.g. episodic summer rain events) (Loik, 2007). In this direction, greater root resistances to cavitation may become associated with a greater capacity of the plant to lift water (Sperry & Hacke, 2002).

Caldwell *et al.* (1998) suggested that a reduction of soil drying rates through HR would extend fine root survival and growth; Bauerle *et al.* (2008) tested this hypothesis using two *Vitis* sp. cultivars. Plants were irrigated on one side only and application of night-time illumination in half the plants stopped HR. They observed that root water potentials were twice as negative in plants where HR was prevented than in plants where HR occurred. The latter had 50% greater root survival in dry soil, and rehydration of fine root tissues through internal HR was responsible for this effect. Since roots engaged in HR live longer, they could take up water and nutrients for an extended time. In addition, these roots do not need to be replaced at a carbon cost

to the plant, which may have relevant implications for plant carbon budget (Bauerle *et al.*, 2008). However, when roots grow old or soil becomes dry, suberization or metacutization of roots (Leshem, 1965; Ryel *et al.*, 2003) could reduce water exchange between soil and roots, and thus reduce or stop HR.

2. Influence of HR on plant nutrient uptake

In the soil matrix, nutrients are found both in a solid phase and in water solution. Microbial activity decomposes soil organic matter, releasing mineral ions that incorporate into the soil solution. Ions need to be transported close to the roots for their absorption and this movement occurs via mass flow, driven by transpiration fluxes, or via diffusion (Nye & Marriot, 1969). Roots are also chemically active at exuding organic carbon, organic anions (P, Fe), protons and phosphatase, fuelling decomposition and increasing nutrient availability (Cardon & Gage, 2006). All these processes depend highly on soil moisture conditions (Tinker & Nye, 2000). It could be hypothesized that increased soil moisture at the surface by HR may maintain nutrients available to plants for longer periods. In an *Artemisia tridentata* stand, HR maintained soil water potentials above the threshold at which nutrient diffusion stops (Ryel *et al.*, 2002), and Matzner & Richards (1996) suggested that the ability of *A. tridentata* shrubs to maintain nutrient uptake under very dry soil conditions (< −5 MPa) was enhanced by release of water through HR, although they did not directly test it. Dawson (1997) showed that nutrient availability increased around roots of plants engaged in HR, nitrogen being the most affected. However, the direct effects on plant nutrient uptake were not tested. There is, however, circumstantial evidence pointing to greater nutrient uptake in dry soils linked to HR, although it was difficult to tell whether nutrient uptake was directly linked to water efflux or to other side-effects (de Kroon *et al.*, 1998; Huang, 1999; Valizadeh *et al.*, 2003; Leffler *et al.*, 2004). Using a different approach, Snyder *et al.* (2008) increased HR rates by artificially suppressing night-time transpiration and observed, however, a trend to lower N uptake in plants with greater HR rates. Overall, a problem common to all these approaches is that either they did not include a true control (i.e. plants not engaged in HR) or nutrients were supplied as liquids, and thus readily available for uptake independently of soil moisture conditions (see Armas *et al.*, 2012).

However, there is ample evidence supporting the idea that HR enhances plant nutrient uptake (Fig. 3). HR effectively enhances organic matter decomposition and thus nutrient mineralization rates, releasing nutrients that could be taken up by plants (Aanderud & Richards, 2009; Armas *et al.*, 2012). Organic matter decomposition rates were 25% greater in dense- than in sparse-root patches under *A. tridentata* shrubs that also had lower soil water potentials (Aanderud & Richards, 2009). This decomposition increase correlated to a threefold greater HR magnitude observed in dense root patches. Organic matter decomposition rates were also 35% higher, and nitrogen mineralization tended to be greater, in soils where buffalograss (*Bouteloua dactyloides*) plants were engaged in HR than in those where HR was prevented (Armas *et al.*, 2012). Enhanced soil moisture and the daily drying–rewetting cycle of HR could create a daily rhythm of root water flux and rhizodeposition that increases microbial activity and decomposition rates (Cardon & Gage, 2006). After > 2 months of drought, buffalograss plants engaged in HR also took up greater amounts of labelled ^{15}N added to the soil as dry organic matter than those with HR prevented (Armas *et al.*, 2012). In a similar study, I. Prieto *et al.* (unpublished) observed greater ^{15}N uptake from nutrient-rich soil patches (dry organic
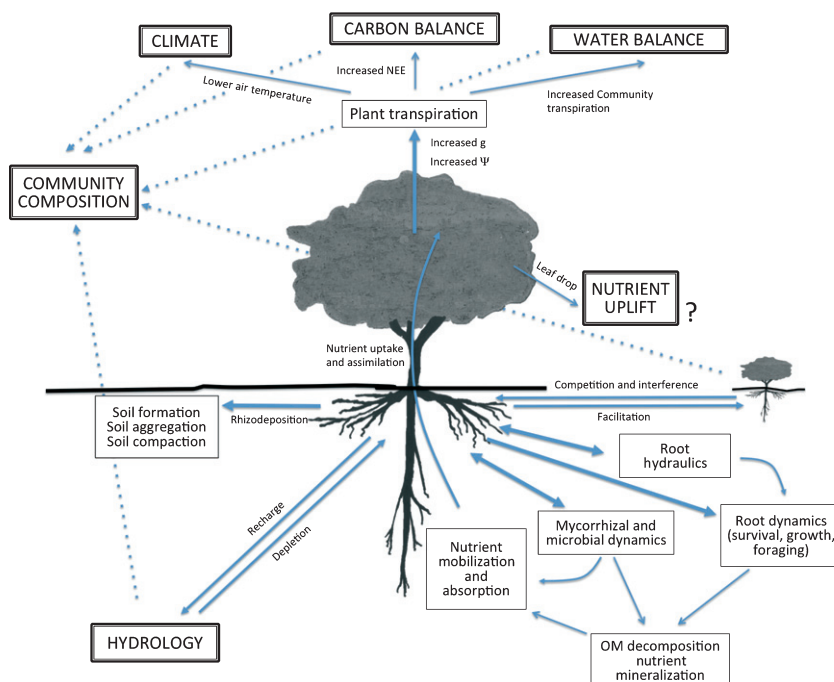

Fig. 3 Schematic representation of above- and below-ground processes. Double boxes, effects at community or ecosystem scale; single boxes, processes; double arrows, water release and absorption; single arrows, direction of processes and sentences next to arrows indicate effects and processes; dotted arrows, processes that could affect plant community composition. NEE, net ecosystem exchange.

matter) in *Retama sphaerocarpa* shrubs that were engaged in HR. Cladode ^{15}N was directly correlated to the amount of water released into dry soil, indicating that HR was responsible for this effect. Hydraulic lift also enhanced root growth in nutrient-rich patches (root foraging precision), suggesting that HR could play a direct role in root foraging strategies. Interestingly, inverse HR (downward HR) has also been involved in nutrient uptake; McCulley *et al.* (2004) used nutrient concentration and stable isotope data to suggest that downward HR might promote the uptake of nutrients stored in deep, dry soil layers where it was otherwise unavailable to plants.

Redistributed water can also move from roots and into the soil via mycorrhizal fungal tips, allowing them to remain active in dry soil conditions (Querejeta *et al.*, 2003). It is hypothesized that this process could indirectly enhance nutrient uptake from dry soils, extending the period of nutrient uptake by plants. Egerton-Warburton *et al.* (2008) tested this hypothesis in *Quercus agrifolia* seedlings growing in split chambers separated by a fine mesh that excluded roots but allowed ectomycorrhizal fungi to grow through. They found that water efflux into the soil in the fungal compartment was correlated to both plant N uptake and soil bacterial abundance and enzymatic activity, suggesting that water released through the extramatrical hyphal mycelia enhanced both plant nutrient uptake and soil microbial processes. Since diffusion of nutrients becomes limited in dry soil, water efflux through mycorrhizal fungi may also increase diffusion rates and thus nutrient uptake by plant roots associated with mycorrhizal fungi (Egerton-Warburton *et al.*, 2008). However, nutrient uptake correlated with plant water uptake because of the presence of ectomycorrhizal fungi and hence the direct role of HR was not clear. These authors proposed two mechanisms by which HR may influence nutrient uptake by plants: an indirect mechanism mediated by increased soil water availability that enhances microbial and enzymatic activity, and a direct role of extramatrical hyphae in maintaining nutrient uptake, as HR in dry soils tends to increase hyphae functionality and likely nutrient diffusion rates (Querejeta *et al.*, 2003, 2007; Lilleskov *et al.*, 2009).

IV. Ecological implications of HR

Hydraulic redistribution acts at the plant level but also influences the structure and function of plant communities (Katul & Siqueira, 2010). In this section we will focus on recent findings of global implications of HR and its importance in structuring plant communities, including its mediation in plant–plant interactions, its influence on biogeochemical cycles and ecosystem-level effects (Fig. 3).

1. Plant–plant interactions

The effect that species engaged in HR have on their neighbours is still unclear. There are reports of positive, neutral or even negative effects depending on ecosystem type, plant life form or whether donor and receiver species shared common ecto- and endomycorrhizal networks (CMNs; Table 2). There are two possible pathways by which neighbouring plants can access water

redistributed overnight by a plant engaged in HR: indirectly from the soil after its release by shallow roots; or directly through CMNs linking different individuals within a plant community (Egerton-Warburton *et al.*, 2007; Warren *et al.*, 2008). This last pathway seems to be the most efficient, as twice as much water was transported between donor and receiver Ponderosa pine trees (*Pinus ponderosa*) directly via CMNs (Warren *et al.*, 2008). In this study, the rate of water transport between large trees and seedlings was high (0.16–0.63 m d^{-1}), which may be an indication that large amounts of water could potentially be transferred through CMNs (in this case, ectomycorrhizal CMNs). However, the relative importance of each pathway on water transport between plants still remains uncertain (Schoonmaker *et al.*, 2007).

Water parasitism has been widely documented in the literature (Caldwell, 1990; Dawson, 1993; Filella & Peñuelas, 2003) and refers to the capacity of understorey species growing next to a species engaged in HR to take up water lifted at night (Caldwell, 1990). The first evidence was obtained by Caldwell & Richards (1989), who observed a similar isotopic signature in water released in upper soil layers through HR by *A. tridentata* shrubs and in stem water of neighbouring *Agropyron desertorum* plants. Since then, evidence of water parasitism has been found in several ecosystems and in plant species with different life forms (Table 2). Deep-rooted species may shed water overnight through HR, potentially benefiting other species, but they also compete with their neighbours for water during the daytime. Ludwig *et al.* (2004) reported an intense competition for water between *Acacia tortilis* and three grass species in its understorey. Grasses effectively took up water redistributed by *A. tortilis* but when tree roots were experimentally removed, preventing access to redistributed water by grasses, the biomass of the latter was greater. Thus, although grasses effectively took up redistributed water, competition between tree and grasses outweighed the potential positive effect of HR. Other studies using grass species have reported similar results (Table 2). However, in mesic ecosystems where water is not as limiting, positive effects have been reported (Dawson, 1993). Grass species usually have shallow root systems (Schenk & Jackson, 2002a) and a great capacity to extract soil water, which makes them great competitors, especially in dry ecosystems where water sources are scarce (Armas & Pugnaire, 2011). In association with a species engaged in HR, the amount of water redistributed may not be enough to meet the grass requirements, and depletion of water by the nurse during daytime would exert a greater negative effect on the grass. In this case, competition would be the predominant outcome of the interaction (Ludwig *et al.*, 2004). On the other hand, grasses usually senesce when soil water potential becomes low and HR may benefit grass species by lengthening the period before soil moisture depletion and senescence occurs (Meinzer *et al.*, 2004), although direct evidence of this effect is scarce (Hirota *et al.*, 2004).

In addition, studies with shrub species living in association with a tree or shrub engaged in HR usually report positive or neutral effects (Table 2). For example, Zou *et al.* (2005) showed differential effects of HR by *Prosopis glandulosa* trees on

Table 2 Summary of earlier works analysing the effects of hydraulic redistribution (HR) on plant–plant interactions in species of similar or different life forms

Sp. engaged in HR	Target species	Growth form	Measured variable	Net effect	Reference
Acer saccharum	*Asarum canadense*	Grass		+	Dawson (1993)
	Fragaria virginiana	Grass		+	
	Podophyllum peltatum	Grass		ND	
	Solidago flexicaulis	Grass		+	
	Thalictrum dioicum	Grass	δD/growth/Ψ_l/g_s	+	
	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		ND	
	Trillium grandifiorum	Monocot		ND	
Acer saccharum	*Acer saccharum*	Tree	δD/g_s	+	Dawson (1996)
Pinus halepensis	*Pistacia lentiscus*	Shrub	δD/δ^{13}C/Ψ_{pd}	+	Filella & Peñuelas (2003)
Acacia tortilis	*Cynodon dactylon*	Grass	δD/Biomass (g)	–	Ludwig *et al.* (2004)
	Panicum maximum	Grass		–	
	Cenchrus ciliaris	Grass		–	
Cajanus cajan	*Zea mays*	Grass	δD	ND	Sekiya & Yano (2004)
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	ND	Brooks *et al.* (2006)
	Tsuga heterophylla	Tree			
	Vaccinium spp.	Shrub			
	Gaultheria shallon	Shrub			
Pseudotsuga meinziesii	*Pseudotsuga meinziesii*	Tree	δD/Biomass/Ψ_{pd}	Neutral	Schoonmaker *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.* (2011)

Results on the facilitative effects of HR are controversial. Positive or neutral effects of HR 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 the study by Dawson (1993). In the latter case, great artificial differentiation between soil layers with a fragipan at 80 cm depth and a groundwater table at a shallow depth greatly enhanced the amount of water redistributed.
δD, deuterium content of xylem water; Ψ_l, leaf water potential; Ψ_{pd}, plant predawn water potential; A, photosynthesis; g_s, stomatal conductance to water vapour; δ^{13}C, leaf isotopic carbon content; F_v/F_m, photosynthetic efficiency of photosystem II. ND, not detected.

neighbouring shrubs that ranged from positive to neutral, concluding that the effect of HR was species-specific. Shrubs are usually deep-rooted and have a less extensive shallow root system than grasses (Schenk & Jackson, 2002a), gaining access to deeper water sources and becoming less dependent on water extraction from shallow layers when these are dry. In this case, depletion of shallow soil water by the tree engaged in HR may exert a small effect on a shrub's performance. Dawson (1993) observed a strong linear relationship between plant growth and the ratio of redistributed water taken up by different understorey species. 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 redistributed water than did shrubs.

Two interesting questions arise concerning HR and plant interactions. The first of these is whether an opposite trend might be seen when the plant is engaged in downward HR. This process may reduce the availability of rainwater to neighbouring shallow-rooted species, although the net effect of such process has not yet been measured. Secondly, it raises the question as to whether water parasitism is the only outcome or whether species engaged in HR also benefit from the association with neighbours, even at the cost of losing some water. Some evidence comes from a case study in southeastern Spain where Prieto *et al.* (2011) observed that, although competition for water was strong among the shrub *Retama sphaerocarpa*, the understorey annuals and *Marrubium vulgare* seedlings, *Retama* facilitated survival of *Marrubium* under its canopy through HR. This positive effect may later indirectly

benefit *Retama* shrubs, as its association with adult *Marrubium* plants improves nutrient uptake and water relations (Pugnaire *et al.*, 1996). Thus, losing a fraction of water redistributed at night may bring an indirect benefit from a species that depends on HR for survival during drought periods.

In summary, neighbours associated with plants engaged in HR seem to benefit from the extra moisture and increased survival rates, and even biomass, which could potentially increase their fitness as they may establish in the community and live long enough to grow and reproduce in subsequent seasons (Prieto *et al.*, 2011).

2. Biogeochemical cycles

Plant-mediated mobilization of nutrients and mineral elements from different soil pools could have broad effects on soil development at the ecosystem scale (Verboom & Pate, 2006). For instance, HR plays an active role in soil-forming processes through translocation of metal compounds under mallee eucalypts (*Eucalyptus incrassata, Eucalyptus pleurocarpa, Eucalyptus decipiens* and *Eucalyptus occidentalis*) growing in a sand dune system in Australia (Verboom *et al.*, 2010). Some metal compounds (Al, Si, and Fe) associated with clay formation in sand dunes were transported from deep soil layers via HR and deposited in shallow soil layers, where they were involved in soil construction around eucalyptus roots.

The downward movement of water through HR could help mobilize nutrients stored at great depths (Walvoord *et al.*, 2003; McCulley *et al.*, 2004; Rumpel & Kögel-Knabner, 2011), indirectly allowing nutrients to be transported upwards to surface layers. Nutrients are usually stored in shallow soil layers but in some arid and semi-arid ecosystems a reservoir of nitrate (NO_3^{-1}) is stored deeper in the soil (Walvoord *et al.*, 2003; but see Jackson *et al.*, 2004). The efflux of water in deep soil layers through inverse HR may help increase nutrient uptake by deep roots (McCulley *et al.*, 2004) and incorporate deep-stored nutrients into plant tissues (i.e. leaves) in a process that may help to increase the rate of 'nutrient uplift' to shallow soil layers when these leaves drop and decompose (Matzner & Richards, 1996; Jobbagy & Jackson, 2004). This 'nutrient uplift' may remobilize nutrient pools that are otherwise inaccessible to the plant community. The mobilization and redistribution of spatially distinct pools of nutrients and other elements via HR may also have broader ecosystem-level consequences related to increased productivity (Liste & White, 2008) and changes in hydrological and biogeochemical cycles (Jackson *et al.*, 2000; Jobbagy & Jackson, 2004; Aanderud & Richards, 2009). Evidence obtained in a semi-arid sand dune system suggests that some salt-tolerant species could release salty water in upper soil layers through HR (Armas *et al.*, 2010). Deep-rooted, salt-tolerant *Pistacia lentiscus* shrubs exerted a negative effect on the performance of salt-intolerant *Juniperus phoenicia* shrubs, caused by the release of salty groundwater into shallow soil layers by *Pistacia*. During the dry season, when HR took place, xylem sap water isotope signature and osmolality were identical in *Juniperus* shrubs growing in close association with *Pistacia* and in *Pistacia* shrubs, whereas sap

characteristics were unique in *Juniperus* shrubs growing alone. Thus, water-soluble compounds like small ions (K^+, Na^+ or Cl^-) could be directly transported by the sap flow and released through HR. Similarly, Salim (1988) showed a net loss of Na^+ from roots and stems tissues to the rhizosphere in *Vigna radiata*. If nutrients or water-soluble ions are redistributed with water, HR could have important consequences for the biogeochemical cycles of some elements.

3. Effects at an ecosystem scale

Plant roots are most dense in the upper 2 m of soil and deep roots usually represent < 10% of the total amount of roots (Canadell *et al.*, 1996; Schenk & Jackson, 2002a,b). Hence, moisture is usually depleted at a faster rate by evaporation and uptake in shallow soil layers. Lifted water, however, can provide a source of soil moisture, which may enhance plant transpiration rates the next day (Caldwell & Richards, 1989). Transpiration increases 10–40% as a result of HR in tropical systems (da Rocha *et al.*, 2004), 20–25% in dry and arid environments (Ryel *et al.*, 2002; Bleby *et al.*, 2010), 19–40% in mesic forests (Jackson *et al.*, 2000) and up to 81% in some Mediterranean ecosystems (Kurz *et al.*, 2006). But what are the main ecological implications for communities? Techniques used to monitor ecosystem gas exchange (eddy covariance towers) and soil and plant physiological parameters along with implementation of results into global gas-exchange models have proved useful at elucidating the implications of HR globally. Lee *et al.* (2005) implemented a soil-vegetation-atmosphere water transfer model in an Amazonian forest that included the phenomenon of HR (Fig. 4). Results showed that water transfer between deep and shallow soil layers overnight increased whole-stand photosynthesis and summer transpiration by c. 40%. Moreover, the upscaling of the model to a global context showed that the cooling effect associated with the increase in plant transpiration and consequent increase in air humidity affected air temperature seasonal cycles, reducing it by > 2°C in most water-stressed regions of the world during the dry season (Lee *et al.*, 2005). The authors concluded that this cooling effect could be underestimated in some dry ecosystems where HR might account for up to 81% of total tree transpiration during drought (Kurz *et al.*, 2006).

Effects of HR on ecosystem carbon balance may also be potentially important. Domec *et al.* (2010) implemented a carbon balance model for a loblolly pine (*Pinus taeda*) forest in North Carolina and included both HR and nocturnal transpiration processes (Fig. 4). They observed a 30–50% HR-mediated increase in whole ecosystem transpiration, which led to an overall increase in plant carbon gain that increased annual gross ecosystem productivity (GEP) and net ecosystem exchange (NEE) by 750 and 400 g C m^{-2} yr^{-1}, respectively. Increases in GEP and NEE maintained the whole forest as a sink for atmospheric carbon. Overall, the presence of HR may have important implications for ecosystem productivity and CO_2 exchange processes in water-limited systems or ecosystems with marked drought periods that could otherwise act as C sources (Domec *et al.*, 2010).
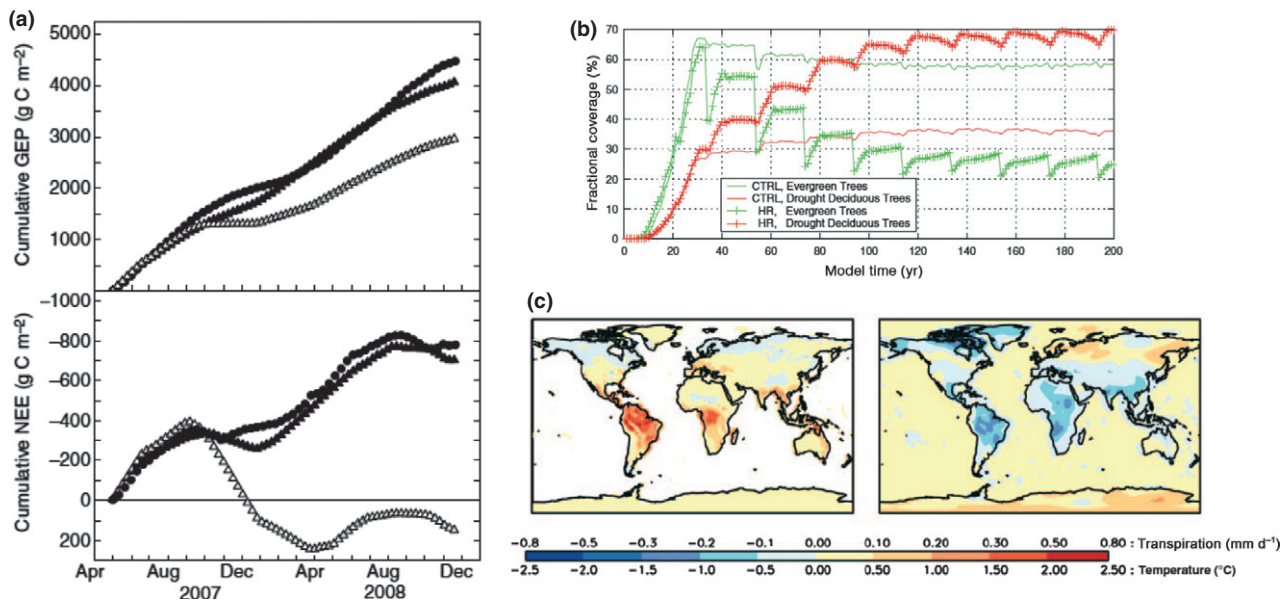
Fig. 4 Global and community effects of hydraulic redistribution (HR). (a) Cumulative net ecosystem exchange (NEE) and gross ecosystem productivity (GEP) in a loblolly pine (*Pinus taeda*) stand in North Carolina (USA). Closed triangles, modelled values with HR; open triangles, modelled values without HR; open circles, measured values. Note how NEE becomes negative in the absence of HR, indicating that the ecosystem acts as a carbon source to the atmosphere. (b) Predicted shift in an Amazonian forest from evergreen (green) to drought deciduous (red) tree dominance in simulation runs that include the effect of HR, whereas in simulation runs without HR (CTRL) evergreen trees are predicted to end dominance of the community. (c) The effect of HR on global transpiration and temperature. Global distribution of the departures of mean annual transpiration (c, left) and mean annual temperature (c, right) in the HR run (communities with plants engaged in HR) from those in the control run (same communities with no HR). (Reproduced from Domec *et al.* (2010), Wang *et al.* (2011) and Lee *et al.* (2005) respectively, with permission from John Wiley & Sons, Inc., Springer Science and Business Media and the National Academy of Sciences (NSA)).

In the long term, increased transpiration rates as a result of HR may also have other ecosystem-level effects. Wang *et al.* (2011) showed a HR-mediated shift in vegetation composition in the Amazonian forests when modelling HR effects during extreme drought periods (e.g. El Niño years, Fig. 4). Water uptake from deep layers and its release into shallow layers accelerated depletion of deep-water reserves during the drought season, causing massive dieback among drought-sensitive evergreen species and replacement with more drought-tolerant deciduous species (Wang *et al.*, 2011). Enhanced transpiration rates may also affect hydrological cycles in temperate forests (Jackson *et al.*, 2000). In these forests, water available for runoff was modelled to be between 3 and 6% lower to reflect enhanced transpiration rates of trees engaged in HR, lowering by several meters the water table as a result of increased plant water consumption from deep layers.

Inverse HR, on the other hand, can affect overall ecosystem water budgets by increasing deep soil water recharge. Water movement to deep soil layers after a rain event is faster through HR than via infiltration or preferential flow and, in the absence of HR, water recharge of deep soil layers would be very low (Ryel *et al.*, 2003). Deep-water recharge through HR accounted for *c.* 10% of the rainwater in a tropical rainforest (Lee *et al.*, 2005) and between 29 and 49% in a *Prosopis velutina* savannah, which supplied 16–49% of drought season transpiration (Scott *et al.*, 2008). Deep-stored water may thus extend the growing season of deep-rooted plants and increase whole ecosystem C gains during drought (Ryel *et al.*, 2002; Scott *et al.*, 2008).

V. Concluding remarks

Throughout the world, HR has been reported in over 60 plant species worldwide and in several biomes, from tropical and temperate forests to arid and semi-arid ecosystems. Recent evidence has suggested that the magnitude and frequency of HR depend on several biotic and environmental factors, resulting in a more complex and heterogeneous process than previously thought. Its effects both above- and belowground are increasingly well understood. Aboveground most of its benefits to individual plants come from increased soil moisture in dry soil layers, which in turn affects plant physiology and water relations. Increased soil moisture enhances root growth and function, and rhizosphere processes such as soil organic matter decomposition or nutrient mineralization rates, which may have relevant implications in ecosystem nutrient cycling.

Plant–plant interactions determine plant community structure and function and, although consequences of HR for neighbouring species are many, evidence shows that provision of water through HR can be a facilitative mechanism in many plant communities where recruitment is mostly restricted to the understorey of adult plants. Shared mycorrhizal networks appear to play a relevant role in water redistribution and in the redistribution of this water among plants, although more evidence is needed on the rates and magnitude of water transfer between adult plants and its ecological consequences.

This review has shown that research not only should focus on HR from an individual plant ecophysiological perspective but

should also try to understand its effects on a wider scale, as this phenomenon has proved to be important at both community and ecosystem levels. Hydraulic redistribution seems to play a role in water and energy fluxes in the ecosystem, and in recent years our knowledge of community- and ecosystem-level effects has improved by incorporating HR processes into hydrological and ecological models. This puts forward the impact of HR on climate and C budgets, increasing overall productivity and maintaining whole ecosystems as carbon sinks. HR may also impact community composition and modify the hydrology of whole watersheds. In a climate change context, the Intergovernmental Panel on Climate Change has predicted a global increase in air temperatures and VPD, along with more infrequent and bigger rain events in dry ecosystems. Under this scenario, increased temperatures and VPDs would ultimately increase water demand by plants, probably leading to the depletion of deep-water reserves that might preclude the occurrence of HR in some ecosystems, reducing the potential buffering effect of HR on surface-air temperatures and C sequestration. Finally, HR should be increasingly taken into account in both hydrological and ecological models as well as in simulations under different climate-change scenarios to fully elucidate its role in net carbon exchange, gross ecosystem productivity, and water budgets and water transfer through the soil–plant–atmosphere continuum.

References

Aanderud ZT, Richards JH. 2009. Hydraulic redistribution may stimulate decomposition. *Biogeochemistry* 95: 323–333.

Allen MF. 2007. Mycorrhizal fungi: highways for water and nutrients in arid soils. *Vadose zone* 6: 291–297.

Armas C, Kim JH, Bleby TM, Jackson RB. 2012. The effect of hydraulic lift on organic matter decomposition, soil nitrogen cycling, and nitrogen acquisition by a grass species. *Oecologia* 168: 11–22.

Armas C, Padilla FM, Pugnaire FI, Jackson RB. 2010. Hydraulic lift and tolerance to salinity of semiarid species: consequences for species interactions. *Oecologia* 162: 11–21.

Armas C, Pugnaire FI. 2011. Belowground zone of influence in a tussock grass species. *Acta Oecologica* 37: 284–289.

Bauerle TL, Richards JH, Smart DR, Eissenstat DM. 2008. Importance of internal hydraulic redistribution for prolonging the lifespan of roots in dry soil. *Plant, Cell & Environment* 31: 177–186.

Bleby TM, McElrone AJ, Jackson RB. 2010. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant, Cell & Environment* 33: 2132–2148.

Brooks JR, Meinzer FC, Coulombe R. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology* 22: 1107–1117.

Brooks JR, Meinzer FC, Warren JM, Domec JC, Coulombe R. 2006. Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations. *Plant, Cell & Environment* 29: 138–150.

Brown RW, Bartos DL. 1982. *A calibration model for screen-caged peltier thermocouple psychrometers*. Ogden, UT, USA: US Department of Agriculture.

Burgess SSO, Adams MA, Bleby TM. 2000. Measurement of sap flow in roots of woody plants: a commentary. *Tree Physiology* 20: 909–913.

Burgess SSO, Adams N, Turner NC, Beverly CR, Ong CK, Khan AAH, Bleby TM. 2001. An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology* 21: 589–598.

Burgess SSO, Adams MA, Turner NC, Ong CK. 1998. The redistribution of soil water by tree root systems. *Oecologia* 115: 306–311.

Burgess SSO, Bleby TM. 2006. Redistribution of soil water by lateral roots mediated by stem tissues. *Journal of Experimental Botany* 57: 3283–3291.

Burgess SSO, Dawson TE. 2004. The contribution of fog to the water relations of *Sequoia sempervirens* (D. Don): foliar uptake and prevention of dehydration. *Plant, Cell & Environment* 27: 1023–1034.

Caldwell MM. 1990. Water parasitism stemming from hydraulic lift: a quantitative test in the field. *Israel Journal of Botany* 39: 396–402.

Caldwell MM, Dawson TE, Richards JH. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113: 151–161.

Caldwell MM, Richards JH. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* 79: 1–5.

Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108: 583–595.

Cardon ZG, Gage DJ. 2006. Resource exchange in the rhizosphere: molecular tools and the microbial perspective. *Annual Review of Ecology, Evolution, and Systematics* 37: 459–488.

Carminati A, Moradi A, Vetterlein D, Vontobel P, Lehmann E, Weller U, Vogel H-J, Oswald S. 2010. Dynamics of soil water content in the rhizosphere. *Plant and Soil* 332: 163–176.

Dawson TE. 1993. Hydraulic lift and the water use by plants: implications for water balance, perfomance and plant–plant interactions. *Oecologia* 95: 565–574.

Dawson TE. 1996. Determining water use by trees and forests from isotopic, energy, balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* 16: 263–272.

Dawson TE. 1997. Water loss from tree roots influences soil water and nutrient status and plant performance. In: Flores HE, Lynch JP, Eissenstat DM, eds. *Radical biology: advances and perspectives on the function of plant roots*. Rockville, MD, USA: American Society of Plant Physiologists, 235–250.

Dawson TE, Burgess SSO, Tu KP, Oliveira RS, Santiago LS, Fisher JB, Simonin KA, Ambrose AR. 2007. Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiology* 27: 561–575.

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507–559.

Domec JC, King JS, Noormets A, Treasure E, Gavazzi MJ, Sun G, McNulty SG. 2010. Hydraulic redistribution of soil water by roots affects whole-stand evapotranspiration and net ecosystem carbon exchange. *New Phytologist* 187: 171–183.

Domec JC, Scholz FG, Bucci SJ, Meinzer FC, Goldstein G, Villalobos-Vega R. 2006. Diurnal and seasonal changes in root xylem embolism in neotropical savanna woody species: impact on stomatal control of plant water status. *Plant, Cell & Environment* 29: 26–35.

Domec JC, Warren JM, Meinzer FC. 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141: 7–16.

Egerton-Warburton LM, Querejeta JI, Allen MF. 2007. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *Journal of Experimental Botany* 58: 1473–1483.

Egerton-Warburton LM, Querejeta JI, Allen MF. 2008. Efflux of hydraulically lifted water from mycorrhizal fungal hyphae during imposed drought. *Plant Signalling & Behaviour* 3: 68–71.

Espeleta JF, West JB, Donovan LA. 2004. Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community. *Oecologia* 138: 341–349.

Espino S, Schenk HJ. 2009. Hydraulically integrated or modular? Comparing whole-plant-level hydraulic systems between two desert shrub species with different growth forms. *New Phytologist* 183: 142–152.

Fernández ME, Gyenge J, Licata J, Schlichter T, Bond BJ. 2008. Belowground interactions for water between trees and grasses in a temperate semiarid agroforestry system. *Agroforestry Systems* 74: 185–197.

Filella I, Peñuelas J. 2003. Indications of hydraulic lift by *Pinus halepensis* and its effects on the water relations of neighbour shrubs. *Biologia Plantarum* 47: 209–214.

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

Grigg A, Lambers H, Veneklaas E. 2010. Changes in water relations for *Acacia ancistrocarpa* on natural and mine-rehabilitation sites in response to an experimental wetting pulse in the Great Sandy Desert. *Plant and Soil* 326: 75–96.

Hao GY, Jones TJ, Luton C, Zhang YJ, Manzane E, Scholz F, Bucci S, Cao KF, Goldstein G. 2009. Hydraulic redistribution in dwarf *Rhizophora* mangle trees driven by interstitial soil water salinity gradients: impacts on hydraulic architercture and gas exchange. *Tree Physiology* 29: 697–705.

Hawkins HJ, Hettasch H, West AG, Cramer MD. 2009. Hydraulic redistribution by *Protea* "Sylvia" (Proteaceae) facilitates soil water replenishment and water acquisition by an understorey grass and shrub. *Functional Plant Biology* 36: 752–760.

Henzler T, Waterhouse RN, Smyth AJ, Carvajal M, Cooke DT, Schäffner AR, Steudle E, Clarkson DT. 1999. Diurnal variations in hydraulic conductivity and root pressure can be correlated with the expression of putative aquaporins in the roots of *Lotus japonicus*. *Planta* 210: 50–60.

Hirota I, Sakuratani T, Sato T, Higuchi H, Nawata E. 2004. A split-root apparatus for examining the effects of hydraulic lift by trees on the water status of neighbouring crops. *Agroforestry Systems* 60: 181–187.

Horton JL, Hart SC. 1998. Hydraulic lift: a potentially important ecosystem process. *Trends in Ecology and Evolution* 13: 232–235.

Howard AR, Van Iersel MW, Richards JH, Donovan LA. 2009. Night-time transpiration can decrease hydraulic redistribution. *Plant, Cell & Environment* 32: 1060–1070.

Huang B. 1999. Water relations and root activities of *Buchloe dactyloides* and *Zoysia japonica* in response to localized soil drying. *Plant and Soil* 208: 179–186.

Hultine KR, Scott RL, Cable WL, Goodrich DC, Williams DG. 2004. Hydraulic redistribution by a dominant, warm-desert phreatophyte: seasonal patterns and response to precipitation pulses. *Functional Ecology* 18: 530–538.

Hultine KR, Williams DG, Burgess SSO, Keefer TO. 2003. Contrasting patterns of hydraulic redistribution in three desert phreatophytes. *Oecologia* 135: 167–175.

Jackson RB, Berthrong ST, Cook CW, Jobbággy EG, McCulley RL. 2004. Comment on "A reservoir of nitrate beneath desert soils". *Science* 304: 51b.

Jackson RB, Sperry JS, Dawson TE. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* 5: 482–488.

Jobbagy EG, Jackson RB. 2004. The uplift of soil nutrients by plants: biogeochemical consequences across scales. *Ecology* 85: 2380–2389.

Katul GG, Siqueira MB. 2010. Biotic and abiotic factors act in coordination to amplify hydraulic redistribution and lift. *New Phytologist* 187: 3–6.

de Kroon H, van der Zalm E, Jan WA, van Dijk A, Kreulen R. 1998. The interaction between water and nitrogen translocation in a rhizomatous sedge (*Carex flacca*). *Oecologia* 116: 38–49.

Kurz C, Otieno D, Lobo do Vale R, Siegwolf R, Schmidt M, Herd A, Nogueira C, Soares David T, Soares David S, Tenhunen J *et al.* 2006. Hydraulic lift in cork oak trees in a savannah-type mediterranean ecosystem and its contribution to the local water balance. *Plant and Soil* 282: 361–378.

Lee JE, Oliveira RS, Dawson TE, Fung I. 2005. Root functioning modifies seasonal climate. *Proceedings of the National Academy of Sciences, USA* 102: 17576–17581.

Leffler AJ, Ivans CY, Ryel RJ, Caldwell MM. 2004. Gas exchange and growth responses of the desert shrubs *Artemisia tridentata* and *Chrysothamnus nauseosus* to shallow- vs deep-soil water in a glasshouse experiment. *Environmental and Experimental Botany* 51: 9–19.

Leffler AJ, Peek MS, Ryel RJ, Ivans CY, Caldwell MM. 2005. Hydraulic redistribution through the root systems of senesced plants. *Ecology* 86: 633–642.

Lehto T, Zwiazek J. 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21: 71–90.

Leshem B. 1965. The annual activity of intermediary roots of the Aleppo Pine. *Forest Science* 3: 291–298.

Lilleskov EA, Bruns TD, Dawson TE, Camacho FJ. 2009. Water sources and controls on water-loss rates of epigeous ectomycorrhizal fungal sporocarps during summer drought. *New Phytologist* 182: 483–494.

Liste H, White JC. 2008. Plant hydraulic lift of soil water – implications for crop production and land restoration. *Plant and Soil* 313: 1–17.

Loik ME. 2007. Sensitivity of water relations and photosynthesis to summer precipitation pulses for *Artemisia tridentata* and *Purshia tridentata*. *Plant Ecology* 191: 95–108.

Ludwig F, Dawson TE, Prins HHT, Berendse F, Kroon H. 2004. Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. *Ecology Letters* 7: 623–631.

Martínez-Vilalta J, Prat E, Oliveras I, Pinol J. 2002. Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. *Oecologia* 133: 19–29.

Matzner SL, Richards JH. 1996. Sagebrush (*Artemisia tridentata* Nutt) roots maintain nutrient uptake capacity under water stress. *Journal of Experimental Botany* 47: 1045–1056.

McCulley RL, Jobbagy EG, Pockman WT, Jackson RB. 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia* 141: 620–628.

McElrone AJ, Bichler J, Pockman WT, Addington RN, Linder CR, Jackson RB. 2007. Aquaporin-mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant, Cell & Environment* 30: 1411–1421.

Meinzer FC, Brooks JR, Bucci SJ, Goldstein G, Scholz FG, Warren JM. 2004. Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types. *Tree Physiology* 24: 919–928.

Moradi AB, Carminati A, Vetterlein D, Vontobel P, Lehmann E, Weller U, Hopmans JW, Vogel HJ, Oswald SE. 2011. Three-dimensional visualization and quantification of water content in the rhizosphere. *New Phytologist* 192: 653–663.

Nadezhdina N, Cermak J, Gasparek J, Nadezdhin V, Prax A. 2006. Vertical and horizontal water redistribution in Norway Spruce (*Picea abies*) roots in the Moravian upland. *Tree Physiology* 26: 1277–1288.

Nadezhdina N, Cermak J, Nadezhdin V. 1998. Heat field deformation method for sap flow measurements. In: Cermak J, Nadezhdina N, eds. *Measuring sap flow in intact plants*. Brno, Czech Republic: Publishing House of Mendel University, 72–92.

Nadezhdina N, David TS, David JS, Ferreira MA, Dohnal M, Tesa M, Gartner K, Leitgeb E, Nadezhdin V, Cermak J *et al.* 2010. Trees never rest: the multiple facets of hydraulic redistribution. *Ecohydrology* 3: 431–444.

Nadezhdina N, Steppe K, De Pauw DJW, Bequet R, Cermak J, Ceulemans R. 2009. Stem-mediated hydraulic redistribution in large roots on opposing sides of a Douglas-fir tree following localized irrigation. *New Phytologist* 184: 932–943.

Nye PH, Marriot FHC. 1969. A theoretical study of the distribution of substances around roots resulting from simultaneous diffusion and mass flow. *Plant and Soil* 30: 459–472.

Paltineanu IC, Starr JL. 1997. Real-time soil water dynamics using multisensor capacitance probes: laboratory calibration. *Soil Science Society of America Journal* 61: 1576–1585.

Prieto I, Kikvidze Z, Pugnaire FI. 2010a. Hydraulic lift: soil processes and transpiration in the Mediterranean leguminous shrub *Retama sphaerocarpa* (L.) Boiss. *Plant and Soil* 329: 447–456.

Prieto I, Martínez-Tillería K, Martínez-Manchego L, Montecinos S, Squeo FA, Pugnaire FI. 2010b. Hydraulic lift through transpiration suppression in shrubs from two arid ecosystems: patterns and control mechanisms. *Oecologia* 163: 855–865.

Prieto I, Padilla FM, Armas C, Pugnaire F. 2011. The role of hydraulic lift on seedling establishment under a nurse plant species in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 181–187.

Pugnaire FI, Haase P, Puigdefábregas J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77: 1420–1426.

Querejeta JI, Egerton-Warburton LM, Allen MF. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* 134: 55–64.

Querejeta JI, Egerton-Warburton LM, Allen MF. 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California oak savanna. *Soil Biology and Biochemistry* 39: 409–417.

Richards JH, Caldwell MM. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73: 486–489.

da Rocha HR, Goulden ML, Miller SD, Menton MC, Pinto LDVO, de Freitas HC, Figueira AMeS. 2004. Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia. *Ecological applications* 14(4 Suppl): 22–32.

Rumpel C, Kögel-Knabner I. 2011. Deep soil organic matter – a key but poorly understood component of terrestrial C cycle. *Plant and Soil* 338: 143–158.

Ryel RJ. 2004. Hydraulic redistribution. In: Esser K, Luttge U, Beyschlag W, Murata J, eds. *Progress in botany*. New York, NY, USA: Springer Verlag, Berlin, Heidelberg, 413–435.

Ryel RJ, Caldwell MM, Leffler AJ, Yoder CK. 2003. Rapid soil moisture recharge to depth by roots in a stand of *Artemisia tridentata*. *Ecology* 84: 757–764.

Ryel RJ, Caldwell MM, Yoder CK, Or D, Leffler AJ. 2002. Hydraulic redistribution in a stand of *Artemisia tridentata*: evaluation of benefits to transpiration assessed with a simulation model. *Oecologia* 130: 173–184.

Salim M. 1988. Loss of sodium from mung bean shoots to saline root media. *Journal of Agronomy and Crop Science* 160: 314–318.

Schenk HJ, Espino S, Goedhart CM, Nordenstahl M, Martinez-Cabrera HI, Jones CS. 2008. Hydraulic integration and shrub growth form linked across continental aridity gradients. *Proceedings of the National Academy of Sciences, USA* 105: 11248–11253.

Schenk HJ, Jackson RB. 2002a. The global biogeography of roots. *Ecological monographs* 72: 311–328.

Schenk HJ, Jackson RB. 2002b. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90: 480–494.

Scholz FG, Bucci SJ, Goldstein G, Moreira MZ, Meinzer FC, Domec JC, Villalobos-Vega R, Franco AC, Miralles-Wilhelm F. 2008. Biophysical and life-history determinants of hydraulic lift in Neotropical savanna trees. *Functional Ecology* 22: 773–786.

Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC. 2002. Hydraulic redistribution of soil water by neotropical savanna trees. *Tree Physiology* 22: 603–612.

Schoonmaker A, Teste F, Simard S, Guy R. 2007. Tree proximity, soil pathways and common mycorrhizal networks: their influence on the utilization of redistributed water by understory seedlings. *Oecologia* 154: 455–466.

Schulte PJ. 2006. Water flow through junctions in Douglas-fir roots. *Plant, Cell & Environment* 29: 70–76.

Scott RL, Cable WL, Hultine KR. 2008. The ecohydrologic significance of hydraulic redistribution in a semiarid savanna. *Water Resources Research* 44: W02440.

Sekiya N, Yano K. 2004. Do pigeon pea and sesbania supply groundwater to intercropped maize through hydraulic lift?–Hydrogen stable isotope investigation of xylem waters. *Field Crops Research* 86: 167–173.

Siefritz F, Tyree MT, Lovisolo C, Schubert A, Kaldenhoff R. 2002. PIP1 plasma membrane aquaporins in tobacco: from cellular effects to function in plants. *The Plant Cell* 14: 869–876.

Smart DR, Carlisle E, Goebel M, Nuñez BA. 2005. Transverse hydraulic redistribution by a grapevine. *Plant, Cell & Environment* 28: 157–166.

Snyder KA, James JJ, Richards JH, Donovan LA. 2008. Does hydraulic lift or nighttime transpiration facilitate nitrogen acquisition? *Plant and Soil* 306: 159–166.

Sperry JS, Hacke UW. 2002. Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology* 16: 367–378.

Steudle E. 2000. Water uptake by roots: effects of water deficit. *Journal of Experimental Botany* 51: 1531–1542.

Tinker PB, Nye PH. 2000. *Solute movement in the rhizosphere*. Oxford, UK: Oxford University Press.

Topp GC, Watt M, Hayhoe HM. 1996. Point specific measurement and monitoring of soil water content with an emphasis on TDR. *Canadian Journal of Soil Sciences* 76: 307–316.

Tyree MT. 1997. The Cohesion-Tension theory of sap ascent: current controversies. *Journal of Experimental Botany* 48: 1753–1765.

Valenzuela-Estrada LR, Richards JH, Díaz A, Eissenstat DM. 2009. Patterns of nocturnal rehydration in root tissues of *Vaccinium corymbosum* L. under severe drought conditions. *Journal of Experimental Botany* 60: 1241–1247.

Valizadeh GR, Rengel Z, Rate WA. 2003. Response of wheat genotypes efficient in P utilisation and genotypes responsive to P fertilisation to different P banding depths and watering regimes. *Australian Journal of Agricultural Research* 54: 59–65.

Verboom WH, Pate JS. 2006. Bioengineering of soil profiles in semiarid ecosystems: the 'phytotarium' concept. A review. *Plant and Soil* 289: 71–102.

Verboom WH, Pate JS, Aspandiar M. 2010. Neoformation of clay in lateral root catchments of mallee eucalypts: a chemical perspective. *Annals of Botany* 105: 23–26.

Walvoord MA, Phillips FM, Stonestrom DA, Evans RD, Hartsough PC, Newman BD, Striegl RG. 2003. A reservoir of nitrate beneath desert soils. *Science* 302: 1021–1024.

Wan C, Xu W, Sosebee RE, Machado S, Archer T. 2000. Hydraulic lift in drought-tolerant and -susceptible maize hybrids. *Plant and Soil* 219: 117–226.

Wang G, Alo C, Mei R, Sun S. 2011. Droughts, hydraulic redistribution, and their impact on vegetation composition in the Amazon forest. *Plant Ecology* 212: 663–673.

Wang X, Tang C, Guppy CN, Sale PWG. 2009. The role of hydraulic lift and subsoil P placement in P uptake of cotton (*Gossypium hirsutum* L.). *Plant and Soil* 325: 263–275.

Warren JM, Brooks JR, Dragila M, Meinzer F. 2011. *In situ* separation of root hydraulic redistribution of soil water from liquid and vapor transport. *Oecologia* 166: 899–911.

Warren JM, Brooks JR, Meinzer FC, Eberhart JL. 2008. Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. *New Phytologist* 178: 382–394.

Warren JM, Meinzer FC, Brooks JR, Domec JC, Coulombe R. 2007. Hydraulic redistribution of soil water in two old-growth coniferous forests: quantifying patterns and controls. *New Phytologist* 173: 753–765.

Yoder CK, Nowak R. 1999. Hydraulic lift among native plant species in the Mojave Desert. *Plant and Soil* 215: 93–102.

Zou C, Barnes P, Archer S, McMurtry C. 2005. Soil moisture redistribution as a mechanism of facilitation in savanna tree-shrub clusters. *Oecologia* 145: 32–40.