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Opinion Paper

Hydraulic redistribution: limitations for plants in saline soils

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Running title: Soil salinity constrains hydraulic redistribution

Abstract

Hydraulic redistribution (HR), the movement of water from wet to dry patches in the soil via roots, occurs in different ecosystems and plant species. By extension of the principle that HR is driven by gradients in soil water potential, HR has been proposed to occur for plants in saline soils. Despite the inherent spatial patchiness and salinity gradients in these soils, the lack of direct evidence of HR in response to osmotic gradients prompted us to ask the question: are there physical or physiological constraints to HR for plants in saline environments? We propose that build-up of ions in the root xylem sap and in the leaf apoplast, with the latter resulting in a large predawn disequilibrium of water potential in shoots compared with roots and soil, would both impede HR. We present a conceptual model that illustrates how processes in root systems in heterogeneous salinity with water potential gradients, even if equal to those in non-saline soils, will experience a dampened magnitude of water potential gradients in the soil-plant continuum, minimizing or preventing HR. Finally, we provide an outlook for understanding the relevance of HR for plants in saline environments by addressing key research questions on plant salinity tolerance.

Brief Summary

Despite significant water potential gradients in saline soils owing to large differences in soil water osmotic potentials within the root-zone of individual plants, no conclusive evidence exists for hydraulic redistribution (HR) in such conditions. This paper advances the hypothesis that build-up of ions in root xylem sap and in the leaf apoplast acts to diminish HR-driving water potential gradients. As a result, plants in spatially heterogeneous saline soils with osmotic-dominated gradients in water potential appear to have little HR.

Introduction

When different parts of the root system of a single plant are subject to contrasting soil water contents, there can be a transfer of water from moist to dry soil via the roots (Richards & Caldwell 1987). This redistribution of water through roots (hereafter referred to as hydraulic redistribution, HR; after Burgess et al. 1998) has been documented in a range of plant species in different ecosystems (Caldwell et al. 1998; Warren et al. 2011; Neumann & Cardon 2012). In a review of representative empirical and modeling studies on HR in 16 different ecosystems, it was found that upward HR from wet to dry soil varies between 0.04 mm and 1.3 mm H_2O d^{-1} (for details see Neumann & Cardon 2012). In drought-prone environments, HR can improve plant performance by: (i) daily movement of a pool of water from roots in moist soil layers to roots in dry soil layers (Caldwell & Richards 1989; Caldwell et al. 1998); (ii) extending the activity and lifespan of fine roots and maintaining root–soil contact in dry soil layers (Brooks et al. 2006; Domec et al. 2004; Bauerle et al. 2008; Scholz et al. 2008); and in the case of downward HR (iii) moving precipitation into deeper soil layers where it does not evaporate (Smith et al. 1999; Burgess et al. 2001; Ryel et al. 2003; Hultine et al. 2004; Scott et al. 2008).

Over the last decade it has become widely recognized that HR, due to the combined effects on soil water content and fine root hydration, influences and ultimately improves the patterns of plant soil water utilization and carbon balance from the single plant level up to the ecosystem level (Domec et al. 2010; Prieto et al. 2012a; Neumann & Cardon 2012). For example, in a loblolly pine (*Pinus taeda*) forest in North Carolina, HR was found to maintain soil water potential above −0.95 MPa in the upper layers, thus limiting the danger of full hydraulic failure by xylem cavitation and allowing the trees to maintain transpiration and photosynthesis through seasonal droughts (Domec et al. 2010). In addition, the water hydraulically redistributed via roots of the pine trees provided the understory species with a supply of water during the early summer when the surface soil started to dry and HR steadily increased (Domec et al. 2010). Furthermore, HR has also been shown to increase plant productivity by enhancing plant nutrient capture not only by increasing soil moisture and hydrating fine roots (e.g., Cardon et al. 2013), but also by increasing root foraging in nutrient rich patches. Soils are generally highly heterogeneous and nutrient(s)-rich patches in soils can correspond to water-depleted patches (Jackson and Caldwell 1993). In a glasshouse experiment using enriched N and P, it was demonstrated that HR could enhance root placement in nutrient-rich patches; as a result, plants with HR had a 25% greater root growth into nutrient-rich patches and a 3 fold increase in ^{15}N uptake compared with plants with impaired HR (imposed by maintaining continuous illumination at night, Prieto et al. 2012b).

Hydraulic redistribution can only occur if a soil water potential gradient exists within the root system of a single plant, and if transpiration is negligible or has ceased (Neumann & Cardon 2012; Prieto et al. 2012a). During the day, transpiration results in the movement of water from the soil to the dry atmosphere via the leaves down a water potential gradient in the soil-plant-atmosphere continuum (Fig. 1). Subsequently at night, once transpiration ceases to be a sink for water movement, then HR can occur. Initially, water potential gradients within roots will drive the internal redistribution of water within the plant, until the root water potential in the dry patches exceeds the water potential of the dry soil (Phase 1 in Fig. 1). As soon as the water potential of the roots in the dry soil exceeds that of the soil, water will flow from these roots to the soil (Phase 2 in Fig. 1; Neumann & Cardon 2012; Prieto et al. 2012a). In theory, root-mediated water flow from wet to dry soil zones will continue as long as water potentials of roots in dry soil remain between the water potential of roots in the distal wet soil and the water potential of the adjacent dry soil. Although the occurrence and role of HR for plants in saline soils has yet to be investigated, based on the known ecological impact of HR in drought-prone environments, in saline ecosystems Phase 1 alone could extend the activity and lifespan of fine roots in more saline patches like for those in dry soil areas (Brooks et al. 2006; Domec et al. 2004; Bauerle et al. 2008; Scholz et al. 2008). Similarly, based on the known ecological impact of HR for plants in drought-prone environments, in saline environments if Phase 2 occurred this could hypothetically: (a) increase long-term transpiration by plants; (b) enhance nutrient uptake; (c) promote the diffusion of salt ions from the rhizosphere to the bulk soil; and (d) if downward HR occurred, increase soil water recharge and storage.

Saline soils have a high degree of spatial heterogeneity, with horizontal and vertical variations in soil salinity across different orders of magnitude within the rooting zone of single plants, due to the interplay of soil leaching and the evapo-concentration of solutes (see Bazihizina *et al*. 2012 and references therein). For instance in field plots with the halophyte *Atriplex amnicola* the salinities of the soil solution (Electrical Conductivity of the soil water; EC_{sw}) within the rooting zone ranged from 40 dS m^{-1} to 120 dS m^{-1} (equivalent to -2 to -6 MPa, Davidson et al. 1996). On the other hand, in a saline cropping field, barley (*Hordeum vulgare*) was found in areas where the EC_{sw} in the rooting zone spanned from 0 to 40 dS m^{-1} (0 to -2 MPa) although in bare areas the EC_{sw} range was substantially higher (44 to 140 dS m^{-1} or -2 to -7 MPa, Richards 1983). This inherent heterogeneity of saline soils is further exacerbated by the fact that plants are affected by the concentration of salts (ions) in the soil solution, which increases hyperbolically as the soil dries, with declines in soil water osmotic potential (i.e. more negative) as well as matric potential, and thus substantial declines in total soil water potential (McFarlane et al. 2017). Therefore, in a similar manner to the ecological importance of HR in drought-prone environments where the heterogeneity in soil water content (matric potential) and thus gradients in soil water potential drive HR, it has been hypothesized that HR could occur and benefit plants in saline environments with heterogeneous soil salinity (osmotic potential gradients) (Hao et al. 2009). To date, however, there has been no clear evidence that HR does occur in response to soil water osmotic gradients both in wet (e.g., wetland) and drier saline environments (Fig. 2), and the potential impact of HR on plant performance in saline environments (when an osmotic gradient dominates) has yet to be evaluated. Indeed, to the best of our knowledge, all studies on HR conducted in saline environments (e.g. Armas et al. 2010; Brooksbank et al. 2011; and several of the studies conducted in the Mono Basin ecosystem in California e.g. Snyder et al. 2008; Aanderud & Richards 2009) suggest that the redistribution of water occurred from moist saline locations to dry but less saline patches (Table 1). For example, using the data from the only study where soil salinity and soil water content were simultaneously measured (see Table 1, Armas et al. 2010), we quantified the relative importance of soil matric potential versus soil osmotic potential in driving HR. To estimate the expected range of each potential, we determined matric potentials (ψ_m) from the measured soil water content (see Table 1) using the water retention curve for sandy soils described by Slatyer & McIlroy (1961), and calculated osmotic potentials (ψ_s) from measured soil EC using the equation:

(i) $\psi_s = ((EC_e*2)*-0.055* SWC_{fc})/SWC$

where EC_e (dS m^{-1}) is the EC of the saturated paste extract of soil, which multiplied by 2 approximates the EC of the soil solution at field capacity (Richards 1954); the factor -0.055 is used to convert dS m^{-1} to MPa (Tavvakoli et al. 2010); SWC_{fc} is the soil water content at field capacity; SWC is the actual soil water content. Total soil water potential (ψ_{total}) was calculated as the sum of the matric and osmotic components:

(ii) $\psi_{total} = \psi_m + \psi_s$

Notably, it emerged that while the gradient in matric potential matched HR direction which moved water from the subsoil to the surface (see Table 1 for results), the osmotic gradient alone would potentially have caused water to move in the opposite direction, from the surface soil to the subsoil (see Table 1). That is, the main driver for HR remained the soil matric potential gradient and not the osmotic (i.e. salinity) gradient. The only other study that estimated HR in an environment where salinity gradients dominated, used sap flow measurements on the halophyte *Rhizophora mangle* (Hao et al. 2009). In this study reverse xylem sap flows (ranging from 0.5 to 2 cm h^{-1}) were measured on most days from 8 pm to 8 am and during low temperature spells in shallow prop roots exposed to an osmotic gradient of 1.0 to 1.5 MPa (Hao et al. 2009); the quantification of reverse sap flow was, however, potentially inaccurate as this study did not verify the zero flow rates in severed roots. Most importantly, definitive evidence of HR is lacking in the above-mentioned study, as no attempt was made to demonstrate water efflux from the roots to the more saline soil area (i.e. Phase 2 in Fig. 1) and reverse sap flow alone could indicate internal redistribution of water involved in rehydration of tissues with lower water status (i.e. Phase 1 in Fig. 1) rather than water loss from roots to the more saline soil (Hultine et al. 2003; Neumann & Cardon 2012).

Given the inherent spatial patchiness of salinity in soils, water potential (i.e. osmotic) gradients in saline soils would seem conducive to HR, yet no conclusive reports exist for HR in these situations (Fig. 2). This prompted us to ask the questions: (i) compared with plants in non-saline soils with gradients in soil water content in which HR occurs, in saline soils are there internal constraints in plants to the transport of water through roots that could limit HR; and (ii) are the gradients in osmotic potential in the plant-soil continuum in saline environments of sufficient magnitude to drive HR?

Constraints to hydraulic redistribution

The main factors affecting HR in drought prone environments have been reviewed elsewhere (Neumann & Cardon 2012; Prieto et al. 2012a) and will only be briefly described here. The essential external condition for HR is that different parts of a plant's root system experience different soil water potentials and that transpiration is very low (i.e. during the night). Rates of water flow from soil to roots and from roots to soil are, however, also influenced by soil hydraulic conductances. Soil texture and water content are the principal factors influencing soil hydraulic conductance, and also soil-root contact, and these factors therefore influence the rates of HR (Neumann & Cardon 2012; Prieto et al. 2012a). In general, coarse textured (i.e. sandier) soils have been found less conducive to HR than finer-textured soils (e.g. clays) (Yoder & Nowak 1999; Wang et al. 2009), which suggests that root-soil contact is more important than soil hydraulic conductance for HR, as sandy soils have higher conductance but less root-soil contact.

Amongst the plant features that affect HR, night-time transpiration, and root architecture and function are key characteristics. Nocturnal transpiration has been found to disrupt HR as the foliage water loss dominates over the roots in the dry soil as the predominant sink for water from roots in the wet soil (Caldwell & Richards 1989; Bauerle et al. 2008; Howard et al. 2009). For example, in a glasshouse study, the artificial suppression of nocturnal transpiration by bagging the shoots of *Artemisia tridentata* and *Helianthus anomalus* increased HR by 73 and 33%, respectively (Howard et al. 2009). Root hydraulic architecture can also strongly influence HR. As HR requires hydraulic integration between the different parts of the root system (i.e. connectivity through xylem connections at the base of roots or the base of the stem), both axial and radial hydraulic conductance will influence rates of flow for a given water potential gradient. Seasonal variations in root hydraulic conductivity have been found to contribute significantly to the variability in HR in a Pacific Northwest coniferous forest; despite the presence of considerable soil water potential gradients that could drive HR, HR declined in the dry season as root hydraulic conductance was reduced due to accumulating embolisms in roots of drought-stressed trees (Warren et al. 2007). Similarly, in the Brazilian savanna, reverse sap flow decreased linearly with reduced root hydraulic conductance and when the water potential gradient between the soil and the roots increased above 0.8 MPa, HR remained nearly constant despite the increase in the driving force due to declining hydraulic conductivities of the roots in the dry season (Scholz et al. 2008).

Internal plant constraints to water transport through roots from low-saline to high-saline patches in soils

The environmental and plant hydraulic conditions required for, and influencing, HR in saline soils could be similar to those in non-saline dry soils. For instance it is likely that salt-induced declines in root axial and radial hydraulic conductivity, observed both in halophytes and non-halophytes under high external salinity (Kapland & Gale 1972; Henzler et al. 1999; Clarkson et al. 2000; Martinez-Ballesta et al. 2003; Boursiac et al. 2005; Sade et al. 2010; Horie et al. 2011; Muries et al. 2011; Sutka et al. 2011), will diminish water outflow from roots to soil and thus reduce HR magnitude. In particular, salinity can result in reduced activity of water channels (aquaporins), which reduces the conductivity of cell membranes and thus also the radial hydraulic conductivity of roots (Tyerman et al. 1999; Maurel et al. 2008; Reef & Lovelock 2014). Nevertheless, as the physiological effects of salinity on plants are not identical to the effects of drought, this raises the question whether there are other additional constraints that could limit or even abolish HR by root systems in saline soils. Unlike situations where virtually only a soil water content (i.e. matric potential) gradient exists in the soil, in saline soils the high concentration of dissolved salts in the soil solution (i.e. osmotic potential) is an overriding component of the soil water potential, so this Opinion Paper therefore focuses on the following aspects in plants in saline soils that may influence HR: (i) ion accumulation in the xylem sap; and (ii) large plant predawn disequilibrium of water potential due to solute accumulation in the shoot.

Xylem osmotic potentials

Uptake of Na^+ and Cl^- by roots in saline solutions results in declines in root xylem osmotic potential; examples for this are available for halophytes (e.g. *Suaeda maritima*, Clipson & Flowers 1987; *Atriplex amnicola*, Galloway & Davidson 1993; *Avicennia germinans* and *Laguncularia racemosa*, López-Portillo et al. 2014) and for non-halophytes (e.g. *Hordeum vulgare*, Greenway 1965, Munns 1985; *Triticum aestivum*, Watson et al. 2001; *Lotus* spp. Teakle et al. 2007). Of particular importance here, xylem osmotic potentials decline more strongly when xylem sap flow rates are low at times of low transpiration, which coincides with the night time when HR is expected to occur. For example, when the halophyte *Suaeda maritima* was exposed to 20, 200 and 400 mM NaCl, Na^+ concentrations in the xylem sap at night increased to values 2 to 4 times those found during the day, which was associated with the lower rate of xylem sap flow at night compared with the day (Clipson & Flowers 1987, Fig. 3a). Increases in xylem sap Na^+ concentrations or decreases in osmotic potential (i.e. more negative) were found also with declining xylem sap flow rates in the non-halophytes *Zea mays*, *Hordeum vulgare* and *Lycopersicon esculentum* (e.g. Greenway 1965; Munns 1985; Jackson et al. 1996; Lopez et al. 2003; Fig. 2). These declines in xylem osmotic potentials during periods of low transpiration are caused by greater decreases in transpiration than in rates of ion uptake; that is xylem flow (and thus the diluting volume) is reduced more than is the rate of 'loading' of ions (Clipson & Flowers 1987; summarised in Fig. 3). Furthermore, at times of low transpirational demand, the asymmetric distribution of influx and efflux carriers within the root and the Casparian strip at the endodermis is thought to prevent backflow of ions from the stele to the apoplast of the cortex (Steudle & Peterson 1998; Robbins et al. 2014). While it is known that loading and retrieval of Na^+ and Cl^- from the xylem comprise both passive and active transport mechanisms that operate at low and/or high external salt concentrations (for more details see Maathuis 2014; Munns & Tester 2008; Li et al. 2017 and references therein), more work is needed to clarify whether the transporters involved have a circadian-regulated expression and whether transpirational demands from the shoot could potentially amplify or alter any diurnal changes and thus xylem loading and the resulting solute concentrations.

Hydraulic redistribution magnitude and duration depends on an outflow of water from roots to soil patches with the lowest water potential. However, in saline soils, if solute accumulation in the xylem leads to substantial decreases in xylem osmotic potentials (e.g. night, Fig. 3), water potential gradients across the soil-root-soil continuum will decrease or even reverse, and without this driving force the outflow of water will cease thus hindering Phase 2 of the HR process (Fig. 1). Furthermore, the strong dependence on the symplastic pathway for water flow across roots of halophytes (e.g. Krishnamurthy et al. 2014) could increase solutes in the xylem at the water exit point as ions are 'filtered' (i.e. expected to be 'excluded' by membranes of cells along the pathway; Passioura 1988) during water backflow to the saline soil. As the distance is too large for substantial diffusion, the solute concentrations in the xylem sap could increase, progressively reducing the water backflow from the roots to the saline soil and thus the driving force for the water transfer between the non-saline and the saline soil patches. Ultimately the xylem osmotic potential would decline to a threshold value at which water exit flow to the saline soil completely stops. This interesting hypothesis was brought forward in the review on water transport by Passioura (1988) to explain the lack of HR in some species in drought-prone environments. Given the demonstrated increases in xylem sap solute concentrations in plants in saline substrates (see previous paragraph), this hypothesis deserves testing, as this mechanism could play a pivotal role in preventing/limiting water loss from roots to a saline soil and thus diminishing HR by roots in saline soils.

Plant predawn disequilibrium of shoot and soil water potentials

Hydraulic redistribution occurs, mainly at night-time, when reduced transpiration increases shoot water potential enabling the soil water potential in dry soil patches to become a sink for water in the plant-soil continuum. In general, predawn shoot water potential is thought to equilibrate closely with water potential of the soil surrounding active roots (Hinckley et al. 1978; Kramer & Boyer 1995; Améglio et al. 1999). However, there can be a significant predawn disequilibrium (PDD) between shoot and soil water potential, which results in the shoot water potential being substantially more negative than the water potential of the soil accessed by the roots (Donovan et al. 1999; Sperry & Hacke 2002; Bucci et al. 2005; James et al. 2006). As HR depends on the water potential gradients established in the plant–soil continuum, PDD will likely affect the internal water redistribution (Phase 1 of the HR process) so that any increases in the water potentials in the roots in the saline soil patches would be dampened (Fig. 1). Although evidence is currently lacking, it is logical to expect that PDD, as reported for night-time transpiration (discussed earlier in this Opinion Paper), could result in the shoot, rather than the roots in the dry soil, becoming the predominant sink for the water from the roots in the wet less saline soil; this would therefore slow the rehydration of the roots in the more saline soil and delay or inhibit the start of Phase 2 of the HR process (Fig. 1).

Although PDD has been found to be nonexistent for small or herbaceous plants, it can be substantial in many woody species and in plants growing in saline environments (Donovan et al. 1999), especially halophytes where PDD can be as large as 2.7 MPa (Donovan et al. 1999, 2001, 2003; James et al. 2006; Lazarus et al. 2011). While PDD is often attributed to night-time transpiration and/or increased resistance in the soil-root-leaf hydraulic pathway, in halophytes it has been associated with high solute accumulation in the leaf apoplast (Donovan et al. 2001; James et al. 2006; Lazarus et al. 2011). Dynamic changes in apoplastic ion concentrations, which have been attributed to solute buildup from daytime transpiration or ion transport between the symplast and the apoplast (James et al. 2006), could enable tissues to regulate cellular water potentials in species that accumulate high concentrations of osmotica (e.g. halophytes) or are subject to fluctuating soil salinity (James et al. 2006; Flowers et al. 2015).

Water potential gradients in the plant-soil continuum: comparison between soil salinity (i.e. osmotic) and soil water (i.e. matric) gradients

Soil water dynamics in an ecosystem will influence the magnitude of HR depending on the combination of soil parameters (e.g. soil texture) with plant morphological and physiological traits (e.g. root architecture, density and mortality, root hydraulic conductivity; Prieto et al. 2010b). The relationship between HR and soil water potential gradients appears to be a bell-shaped curve, with minimal values at the extremes of the range and higher values mid-range (Fig. 4a). Numerous field studies suggest that HR only starts after drying soils reach a certain water potential threshold (generally −0.4 to −0.8 MPa, Neumann & Cardon 2012). Subsequently, HR increases with increasing gradients until the water potential in the dry soil reaches a critical point where HR declines with further decreases in soil water potentials due to declines in root and/or soil hydraulic conductivity (Fig. 4a; Brooks et al. 2002; Domec et al. 2004, 2006; Meinzer et al. 2004; Warren et al. 2007; Prieto et al. 2010a; Neumann et al. 2014).

As observed for soil water (matric potential) gradients, it could be predicted that a similar bell-shaped relationship occurs for HR by root systems experiencing soil salinity (osmotic potential) gradients (Fig. 4b,c). The magnitude of these osmotic gradients, however, can be expected to be smaller than those of matric potentials in drying soils due to ion accumulation in the xylem and plant apoplast, which would reduce water efflux from roots in the more saline soil, minimizing HR or even preventing it (see preceding sections of this Opinion Paper). Indeed the concurrent declines in xylem osmotic potentials and the accumulation of ions in tissues at the site of water exit in the xylem will reduce the water potential gradient between the roots and the soil in the saline patches, which in turn could limit if not completely stop water backflow from the roots to the saline soil, reducing HR magnitude and narrowing the water potential ranges at which HR can occur (Fig. 4b,c). On the other hand, large PDD due to the accumulation of solutes in the leaf apoplast would also substantially narrow the range at which HR can occur; indeed, HR would begin only if the water potential in the roots in the saline soil patches declined below the predawn water potential in the leaves, which for leaves of some halophytes has been found to be as low as -3.65 MPa (James et al. 2006). Until then, the greater water potential gradient in the soil-plant continuum between the leaves and the soil would result in water moving predominantly towards the leaves, slowing the rehydration of the roots in the saline soil (Fig. 4b,c). HR magnitude is expected to decline not only in moist saline environments where gradients are osmotic owing to differences in salinity between soil layers or patches (Fig. 4b) but also in drought-prone saline environments where soil water (i.e. matric) gradients also occur and can even dominate over osmotic gradients. Indeed, in these drier environments, for example with a saline water table accessed by roots at depth, HR would only occur if the water potential of the dry part of the soil declined below the water potential in the moist but saline parts (Fig. 4c). In addition, the high ion concentrations in the moist soil part and ion entry to the xylem, as for HR in response to salinity gradients alone, would substantially decrease xylem osmotic potentials and also likely result in large PDD, which would further reduce HR magnitude in plants in saline soils even with a soil water content (i.e. matric potential) gradient.

Conclusions and outlook for future research

Hydraulic redistribution can play an important role for individual plants up to the ecosystem level in drought-prone environments (Domec et al. 2010; Burgess 2011; Prieto et al. 2012a). By contrast with these situations in which water potential gradients are dominated by differences in soil matric potential, we propose that HR is very limited in plants in saline environments where differences in soil salinity result in external osmotic gradients. Specifically, in this Opinion Paper, we addressed two key questions: (i) are there additional plant internal constraints to HR in saline soils; and (ii) are the osmotic gradients in the plant-soil continuum in saline environments of sufficient magnitude to drive HR? Although our ability to definitively answer these questions is limited by gaps in knowledge as identified in this Opinion Paper, we advance the hypothesis that HR is unlikely to provide an immediate benefit to plant productivity in spatially heterogeneous saline soils, where osmotic gradients are an important component of the soil water potential gradient within the root zone. The accumulation of ions in plants, which decreases the osmotic potential of the xylem sap of roots and can result in large PDD between shoots and roots, is likely to reduce the driving force for water backflow from the roots to the saline soil and thus HR. It is however important to determine the relative importance of the different phases of HR in saline environments. Currently in the literature dealing with HR in saline soils there is no conclusive evidence of water backflow into the soil; future work should clarify HR events with ‘root-mediated redistribution of soil water’ (i.e. water flows into soil) as well as situations with transient ‘reverse flow’ which rehydrates distal tissues but without water backflow to the soil. Indeed, while the impact of HR in saline environments is likely to be minimal, it is important to note that the internal redistribution of water likely does occur in at least some plants in saline systems (e.g. Hao et al. 2009; Shelef et al. 2016). This internal redistribution of water is likely to aid root survival in saline soils (as observed under drought conditions, Bauerle et al. 2008) and so would be physiologically and ecologically significant, and could potentially have important management implications (such as crop selection and irrigation management) in these saline landscapes that are inherently highly heterogeneous in time and space for levels of soil salinity.

Salt loading into the xylem has long been considered one of the key determinants of salinity tolerance in plants (non-halophytes and halophytes; Tester & Davenport 2003; Munns & Tester 2008; Flowers & Colmer 2008; Shabala et al. 2013; Zhu et al. 2016; Li et al. 2017). Although some transport mechanisms for Na^+ and Cl^- loading and retrieval at the soil-root and stelar cell–root xylem vessel interfaces are known or have been proposed (Munns & Tester 2008; Li et al. 2017), no knowledge of the regulation of these transporters is currently available for plants with roots exposed to heterogeneous salinities. In particular, additional work is needed to improve our understanding of diel changes of ion concentrations in the xylem sap in each root section exposed to the various levels of salinity and at the whole plant level, and how the ion transport processes are affected/regulated by transpiration and/or by light/diurnal rhythms (e.g. as seen for NO_3^- or NH_4^+ transporters, Lejay et al. 1999 and the diurnal changes in aquaporin expression, Lopez et al. 2003; Vandeleur et al. 2009). Glasshouse and field studies are required to unravel how heterogeneous salinities affect levels of apoplastic solutes in roots and the shoots, and whether the strong dependence on the cell-to-cell pathway of radial water movement across roots could cause an increase in xylem solutes if water flows from the xylem to the external medium (*cf.* Passioura 1988). The knowledge of solute dynamics in xylem and the apoplast will be crucial to improve our mechanistic understanding of how soil salinity affects HR in plants in saline soils in various environments, including wetland, mesic and drought-prone areas. In particular, comparisons should be made between (and within) non-halophytic and halophytic species with different abilities to regulate their xylem ion compositions and tissue water relations.

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Table 1. Vertical variation in soil solution salinity and soil water content in different saline environments where root-mediated redistribution of soil water or transient “reverse flow” (i.e. without water backflow into the soil) from the subsoil to the surface soil was detected.

Environment	Surface soil			Subsoil			Comments	Reference
	Soil salinity (EC_{sw}, dS m^{-1})[a] (Ψ_s, MPa)	Water content (m^3 m^{-3}) (Ψ_m, MPa)[c]	Soil water potential (Ψ_{total}, MPa)	Soil salinity (EC_{sw}, dS m^{-1})[a] (Ψ_s, MPa)	Water content (m^3 m^{-3}) (Ψ_m, MPa)	Soil water potential ($\Psi_{\mathbf{total}}$, MPa)		
Studies specifically conducted to study HR in saline environments								
Coastal dune system	**0.6** -0.95[b]	**< 0.004**[c] < -0.72[d]	<-1.67	**25.7** -1.41[e]	**0.18**[c] >-0.03[d]	>-1.44	Root-mediated redistribution of soil water detected by monitoring stem-water isotopes signature in two interacting shrub species with contrasting rooting system	Armas et al. 2010
Mangrove forest	22.7-32.7[e] **-1.2 to -1.8**	nd nd	nd	4.5-7.3[e] **-0.2 to -0.4**	nd nd	nd	Transient reverse flow detected using heat pulse sap flow probes	Hao et al. 2009
Studies conducted in saline environments without the aim to investigate how salinity affects HR								
Dryland farming	**2.4-3.4** nd*	**≤ 0.04** < -1.5[f]	nd	**4.4-5.4** -0.24 to -0.30[e]	**0.16-0.28** ≥-0.03[f]	>-0.33	Transient reverse flow detected using heat pulse sap flow probes	HR data, soil water content and groundwater EC from Brooksbank et al. 2011. Soil salinity from Carter & White 2009
Dune complex in a Mono Basin ecosystem	**0.2-1.2**[g] nd	nd nd	**-0.4 to -3.7**[h]	nd nd	nd nd	nd	Root-mediated redistribution of soil water detected by monitoring soil water potentials and temperature using thermocouple psychrometers	HR from Aanderud & Richards 2009 Soil salinity from Aanderud et al. 2008

In all studies the reverse flow (without water backflow into the soil) or root-mediated redistribution of soil water occurred from the subsoil (> 50 cm) to the surface soil (0-50 cm). OP, osmotic potential; MP, matric potential; EC_{sw} – EC of the soil solution. Bold numbers refer to data measured in each study and light numbers to estimated values. [a]EC_{sw} was estimated assuming that it is ~2-times the saturated soil extract (EC_e) for soils at field capacity (Richards 1954) and conversions from $EC_{1:5}$ to EC_e were made according to soil texture (sand to sandy clay) using the factors in Slavich & Petterson (1993). [b]Conversions to soil osmotic potentials (MPa) has been made based on soil water content and soil salinity using formula (i) described in the text. [c]Conversion from soil gravimetric water content (%) to soil volumetric water content (m^3 m^{-3}) was done assuming a soil bulk density for sands of 1400 kg m^{-3} (Li et al. 2003). [d]Conversion from soil water content to matric potential and *vice versa* was made according the water retention curve for sandy soils described by Slatyer & McIlroy (1961). [e]For groundwater data and saturated soils conversions to osmotic potentials (MPa) or *vice versa* has been made assuming that 100 mM NaCl ≅ 10 dS m^{-1} ≅ -0.55 MPa (Tavvakoli et al. 2010). [f]Conversion made assuming that field capacity of the soils was 0.16 m^3 m^{-3} and wilting point was 0.05 m^3 m^{-3} (Brooksbank et al. 2011). [g]ECe was calculated based on measured Cl^- concentrations and assuming that all salts were NaCl. [h]Total soil water potential (the sum of the matric and osmotic components) was measured using thermocouple psychrometers. *Soil osmotic potential was not estimated as soil salinity and water content were not simultaneously measured and have been taken from different studies (see Table for more details). Ψ_s, Osmotic potential; Ψ_m, Matric potential; Ψ_{total}, Total soil water potential; nd, not determined.

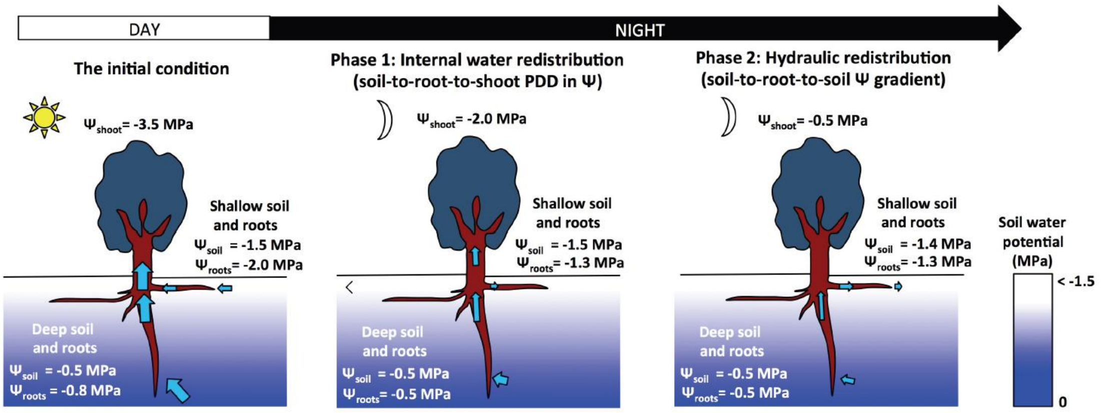

Figure 1. Schematic diagram of day and night water movement within the plant, assuming typical soil and plant water potentials with hypothetical values for soil, root and shoot water potentials. Hydraulic redistribution within a plant will occur if there is a soil water potential gradient within the root system and can be divided into two phases. The initial condition results from plant transpiration that will create a water potential gradient in the soil-plant-atmosphere continuum. In Phase 1, once transpiration ceases to be the main sink for water movement, water potential gradients within roots will drive the internal redistribution of water within the plant, until the root water potential in the dry location exceeds that of the dry soil. Arrows show the dominant water flow direction. In Phase 2 the higher water potential in the roots compared to those in the dry soil will result in water backflow from the roots to the soil. Arrows show the dominant water flow direction. Ψ= Water potential; PDD= Plant predawn disequilibrium.

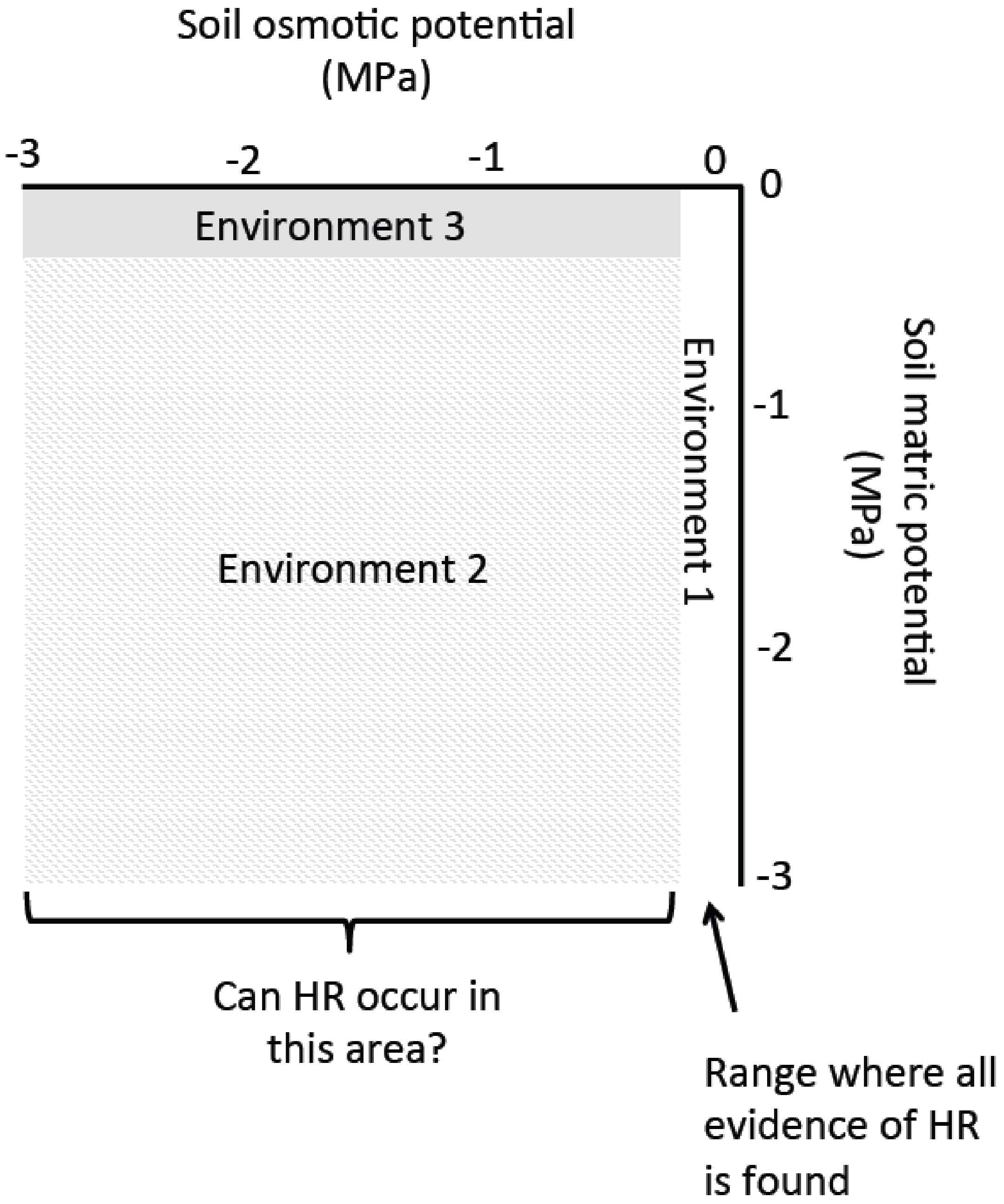

Figure 2. Range of water content and salinity gradients in soils where HR could theoretically occur and where evidence of HR has been found. Environment 1 – contrasts in water content in different soil layers are the main driver of the water potential gradients; Environment 2 – both water content and salinity differences are drivers of the water potential gradients; Environment 3 – soil salinity contrasts are the main driver of the water potential gradients.

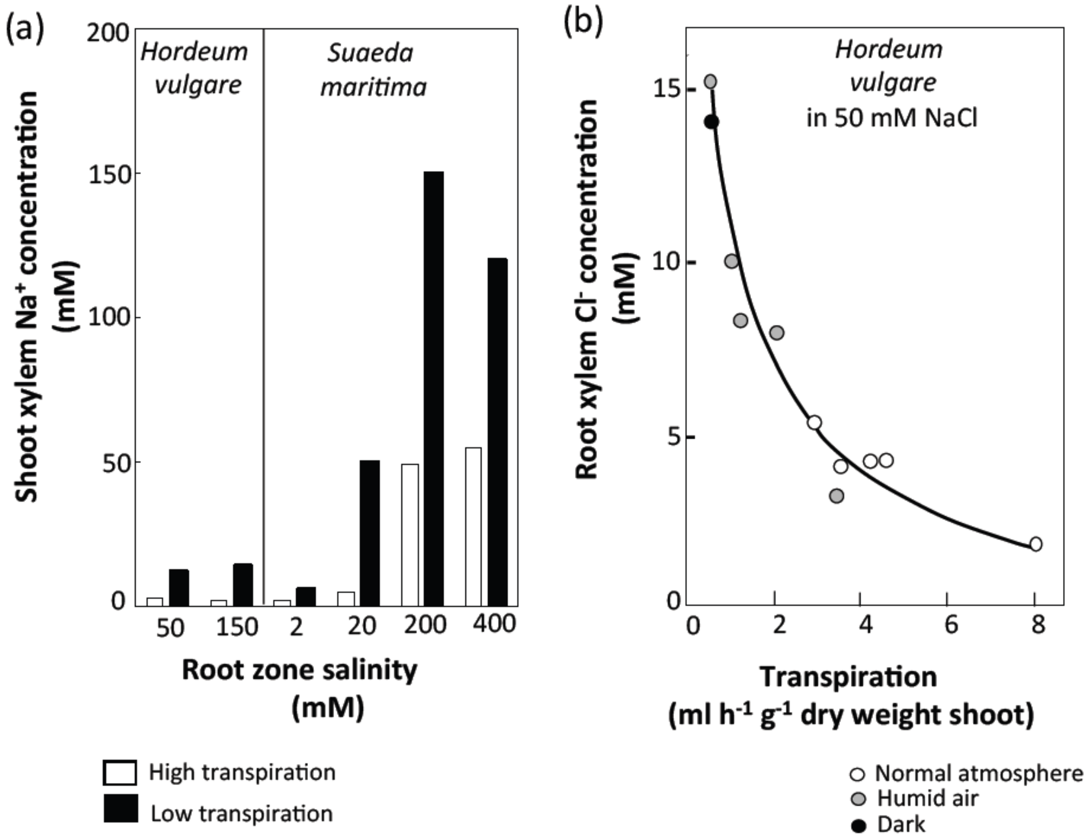

Figure 3. Examples of xylem ion concentrations (i.e. influencing xylem osmotic potential) in relation to plant transpiration and root-zone salinity (NaCl). (a) Effect of transpiration and root-zone salinity on Na^+ concentration in shoot xylem of a salt-tolerant non-halophyte (*Hordeum vulgare*, drawn from data in Munns (1985), with permission from Wiley Publishing) and a halophyte (*Suaeda maritima*, reproduced from Clipson & Flowers (1987), with permission from Wiley Publishing); (b) Effect of transpiration on Cl^- concentration in root xylem of *Hordeum vulgare* grown with 50 mM NaCl in the root-zone (reproduced from Greenway (1965), with permission from CSIRO Publishing).

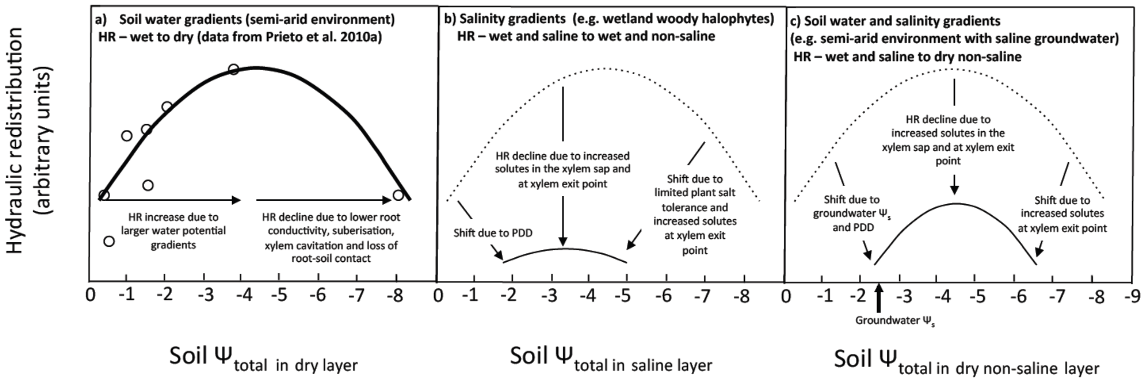

Figure 4. Predicted magnitude of hydraulic redistribution (HR) in saline environments as a function of soil water potentials based on comparison with hydraulic redistribution in *Retama sphaerocarpa* shrubs in a drought-prone environment (Prieto et al. 2010a). (a) Reproduces data from Prieto et al. (2010a) with permission from Springer Publishing to provide the relationship between HR and soil water potentials in the top 50 cm (i.e. drier soil layer in the soil column) of soil under the shrubs; (b) the hypothesised relationship between HR and gradient in soil water osmotic potential in wet saline environments (i.e. wet saline to wet less/low saline or non-saline); (c) the hypothesised relationship between HR and gradient in soil water potential in drought-prone saline environments (i.e. wet saline to dry less/low saline or non-saline). Ψ_s = Osmotic potential; PDD = Plant predawn disequilibrium; Ψ_{total} = Total water potential (the sum of the matric and osmotic potentials). The dashed line in (b) and (c) represent the relationship between HR and soil water potentials shown in (a). The lines in (b) and (c) represent, respectively, the hypothesised relationship between HR and soil water potential in the saline and drier soil layer of the soil based on comparison with relationship in (a).