

OPINION PAPER

The significance of roots as hydraulic rheostats

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Abstract

Roots are the primary sites of water uptake by plants. Roots also sense most of the physico-chemical parameters of the soil, perceive signals from the shoots, and adjust their growth and water transport properties accordingly. The present opinion paper discusses the significance of the variable water transport capacity (hydraulic conductance) of roots during development and in response to environmental stimuli. It is shown that root hydraulics determines water uptake intensities but also water potential gradients within the plant. It is indicated how the dynamics of root hydraulics contributes to many integrated plant nutritional and growth functions. For instance, the heterogeneity of soil water and nutrient availability and the heterogeneity of root hydraulic properties feed each other and play critical roles in root transport functions. Another important aspect is the integration of root hydraulics within the mutual interactions of roots and shoots, for co-ordinated growth and water-saving responses to drought.

Key words: Aquaporin, drought, nutrient, root, soil water, water uptake.

Introduction

Roots are the primary sites of water uptake by plants. Roots also have a remarkable capacity to sense most of the physico-chemical parameters of the soil and to adjust their growth and water transport properties accordingly; these functions being tightly linked to shoot physiology. Roots, therefore, play a central role in maintaining the water status of the whole plant in a changing environment.

Many facets of root hydraulics have been investigated in detail. One facet concerns the cell and tissue paths followed by water during uptake. Theoretical models which explain the relative contribution of concentric cell layers to whole root hydraulics and some of its functional properties have been proposed (Steudle and Peterson, 1998; Javot *et al.*, 2003; Bramley *et al.*, 2009). Another facet concerns the function of roots as an hydraulic rheostat, that is, the dynamic changes in their hydraulic resistance that occur during development and in their responses to environmental stimuli. In recent years, the various molecular and biophysical mechanisms that underlie

these changes have been extensively studied and covered by several reviews (Steudle and Peterson, 1998; Javot and Maurel, 2002; Vandeleur *et al.*, 2005; Martinez-Ballesta *et al.*, 2006; Maurel *et al.*, 2008). Surprisingly, the physiological significance of these regulations has remained rather elusive.

In the soil–plant–atmosphere continuum, the predominant resistance to water transfer is contributed, at the leaf–atmosphere interface, by both the stomata and boundary layers, which therefore determine the rate of transpiration for a given evaporative demand. In this representation, the hydraulic resistance of internal plant tissues is minor and roots contribute to it by only one-third to one-half (Simonneau and Habib, 1991; Javot and Maurel, 2002). The present opinion paper intends to discuss the significance in whole plant physiology of the root hydraulic resistance and why this resistance is variable and under such tight physiological control. Our speculations integrate root hydraulics within root-to-soil interactions and link it to

other root and shoot functions. They will hopefully promote novel investigations in integrative plant biology.

The fundamentals of root hydraulics

Water transport paths and the role of aquaporins

This section provides the reader with a short outline of the biophysical and molecular bases of root water uptake, with the minimal background required for the following discussion. Extensive reviews on root water uptake can be found elsewhere (Steudle and Peterson, 1998; Steudle, 2000; Javot and Maurel, 2002; Vandeleur *et al.*, 2005; Maurel *et al.*, 2008). During this process, soil water first flows radially through living tissues (epidermis, cortex, endodermis, and stele) to reach the xylem vessels. The resulting sap is then transported axially to the aerial parts of the plant. Except in the root tips, xylem vessels have a much lower hydraulic resistance than the living peripheral tissues (Steudle and Peterson, 1998). In these tissues, water flows radially through the cell wall continuum (apoplastic path) or from 'cell-to-cell', through cytoplasmic continuities (symplastic path) or by crossing cell membranes (transcellular path). These notions have led to a representation of the root as concentric cell layers acting as hydraulic resistances in series, each layer containing apoplastic and cell-to-cell hydraulic resistances working in parallel. This so-called composite model represents a reference formalism in which to integrate the emerging properties of root hydraulics. In particular, state-of-the-art biophysical analyses of whole roots have revealed specific force-to-flow relationships or water-to-solute selectivities that can typically be explained using the composite model (Steudle, 1994).

In certain species, the transcellular path can play a major role as it is efficiently facilitated by water channel proteins named aquaporins. These proteins belong to the ubiquitous superfamily of Major Intrinsic Proteins (Maurel *et al.*, 2008). The structure at an atomic resolution of several aquaporins including spinach *SoPIP2;1* (Törnroth-Horsefield *et al.*, 2006) has shown how these proteins are inserted as tetramers in the membrane to form four individual pores which allow the passage of water or of small neutral molecules (Maurel *et al.*, 2008). In plants, aquaporins fall into four or five homology subfamilies, among which the Plasma membrane Intrinsic Proteins (PIPs) represent the most abundant aquaporins at the plasma membrane. Because this membrane is a potential obstacle to transcellular water flow, PIPs can control a large part of the root water permeability or hydraulic conductivity (L_p) (Siefritz *et al.*, 2002; Tournaire-Roux *et al.*, 2003). The conductance (L_0), which integrates L_p and the root surface, represents the water uptake capacity of the whole root system.

The dynamics of root hydraulics and aquaporin regulation mechanisms

A large array of environmental and hormonal stimuli are known to trigger short-term (minutes to hours) adjustments of L_p . Drought and salinity stresses, which are the most

extensively studied stimuli, usually induce a marked drop in L_p whereas ABA can exert either an up- or a down-regulating effect, depending on time, dose or species (Hose *et al.*, 2000; Martinez-Ballesta *et al.*, 2003; North *et al.*, 2004; Parent *et al.*, 2009). Soil compaction or flooding which restrict oxygen diffusion in the soil, result in root anoxia which, in turn, down-regulates L_p in certain plant species (Tournaire-Roux *et al.*, 2003; Bramley *et al.*, 2010). The availability in the soil of mineral nutrients such as nitrate or phosphate also influences root hydraulics (Clarkson *et al.*, 2000; Gorska *et al.*, 2008). Nutrient starvation usually induces a progressive drop in L_p whereas a supply of nutrient results in its rapid up-regulation. Light is also a major regulator of plant hydraulics. Diurnal variations in root water uptake are usually associated with an up-regulation of L_p during the day (Clarkson *et al.*, 2000).

There is now substantial pharmacological and genetic evidence that most of the short-term changes in root hydraulics are mediated through the regulation of root aquaporin expression and activity. A variety of mechanisms involving transcriptional control (Maathuis *et al.*, 2003; Alexandersson *et al.*, 2005), stimulus-induced internalization of PIPs (Boursiac *et al.*, 2008a), or regulated channel opening and closing (gating) by cytosolic calcium, cytosolic protons, or aquaporin phosphorylation has been revealed (Tournaire-Roux *et al.*, 2003; Törnroth-Horsefield *et al.*, 2006; Boursiac *et al.*, 2008b; Verdoucq *et al.*, 2008). It is of note that most of the soil stress conditions, including cold and water, nutrient or oxygen deprivation, all influence L_p and induce an accumulation of reactive oxygen species (ROS) in root tissues. A conserved signalling chain involving ROS and acting downstream on aquaporin phosphorylation and subcellular re-localization mediates, in part, the down-regulating effects of these stresses on L_p (Boursiac *et al.*, 2008a, b). A ROS-induced stimulation of L_p has also been reported in certain plant species (Benabdellah *et al.*, 2009).

In the long term, environmental or hormonal stimuli act on root growth and differentiation thereby adding another controlling level of root hydraulics. Water stress, for instance, can induce the differentiation of an exodermis or an endodermis with lower apoplastic permeability due to enhanced suberin deposition (Zimmermann *et al.*, 2000; Vandeleur *et al.*, 2009) and the proliferation of specialized side roots (Vartanian *et al.*, 1994). Nutrient deprivation usually enhances overall root growth for the improved exploration of enriched or new soil horizons (López-Bucio *et al.*, 2003). Thus, environmental stresses can modify the hydraulic conductivity of apoplastic barriers and overall exchange surfaces. These anatomical and architectural changes can be accompanied by an adjustment of the aquaporin equipment, which may explain the long-term effects of stresses on aquaporin gene expression.

Control of flow versus control of water potential

In many studies on water transport, physiologists work with experimentally controlled driving forces and associate the

hydraulic conductivity of isolated cells or excised organs to water flow intensity. This representation may be misleading when it is extrapolated as such to the whole plant. Under transpiring conditions, for instance, the resistance to water transfer of the stomata and boundary layers largely dominates all upstream resistances acting in series and determines the rate of water flow moving through the plant body. Thus, in this context, the root and other internal resistances should not be interpreted as being exclusively important for determining water flow intensity. They may also control the profile of water potential gradients throughout the plant. Leaf water potentials of sunflower plants, measured and modelled in relation to changing hydraulic conductance and transpiration, typically illustrate these properties (Tsuda and Tyree, 2000)

Figure 1 describes a representative experiment on transpiring maize plants grown in hydroponics in a split root system. The hydraulic conductivity of one half of the root system was reduced by acid loading, a strong aquaporin inhibiting treatment (Tournaire-Roux *et al.*, 2003). Despite this, water uptake by the whole root remained constant. Yet, the absorption rate by the treated root half was markedly reduced whereas that of the untreated root half was increased (Fig. 1B). The explanation for this is that, at the whole root level, a reduction in L_p in conditions where the water uptake rate was maintained resulted in a drop in xylem water potential (Ehlert *et al.*, 2009). This created a compensating driving force, which explains the increase in absorption rate by the untreated root half.

This example indicates that when interpreting the significance of variable root hydraulic properties, it is crucial to

distinguish between contexts where the variable root properties are directly responsible for a change in water flow intensity and others where they are not. In the latter case, root hydraulics primarily impacts on water potential profiles and, therefore, can also be crucial for the whole plant water status. The example in Fig. 1 also indicates the importance of considering the root and/or the soil as heterogeneous systems.

Roots and the optimization of soil water usage

An adjustable L_p can first be considered from a purely hydraulic point of view as a means for optimizing soil water use. In these respects, the response of plants to drought offers a first interesting context to examine. It was proposed that a transient increase in L_p during the onset of drought (as mimicked by exposure of roots to exogenous ABA) may provide the means for capturing residual water in the drying soil (Hose *et al.*, 2000). The long-term down-regulation of L_p in droughted plants would, by contrast, be interpreted as a survival reaction to postpone soil water shortage under prolonged stress. Whereas plants with reduced transpiration overcome periods of drought better (Iuchi *et al.*, 2001), there is, however, no evidence that a lowered root capacity to extract soil water would provide such an advantage. A reduction in L_p may primarily impact on water potential gradients along the soil–root–shoot continuum, thereby inducing water-saving reactions in the leaves, as discussed later. Drought-induced inhibition of L_p can, however, directly induce changes in water uptake in soils with a non-uniform water distribution. In such conditions, a reduction of L_p in roots exposed to low water availability would lead to a lowering of soil water uptake by these roots. Yet, the roots of the plant exposed to other horizons would compensate by increasing their water uptake due to a decrease in xylem water potential, as exemplified in Fig. 1 (Simonneau and Habib, 1994; Ehlert *et al.*, 2009). One advantage of this mechanism is that it may help the sub-fraction of the roots exposed to the driest soil zone to survive, without hampering the overall water uptake capacity of the plant.

Down-regulation of L_p can also be a protective reaction to restrict a possible backflow of water from the plant into the most desiccated zones of the soil, especially at night in the absence of any transpirational driving force (Caldwell *et al.*, 1998; Jackson *et al.*, 2000; Doussan *et al.*, 2006). The above-mentioned strategy of increasing L_p in response to ABA is therefore at risk of facilitating a backward flow of water from the plant into the soil, if the plant cannot maintain an adequate water potential gradient. The most exposed plants would be those with thin roots and thereby a high exchange area relative to root mass, such as *Arabidopsis*. This may explain why this species apparently lacks any response of L_p to ABA. A plant-to-soil backflow of water has actually been observed under drought conditions, but in the most superficial layers of the soil (Caldwell *et al.*, 1998). As soil water was taken up by the

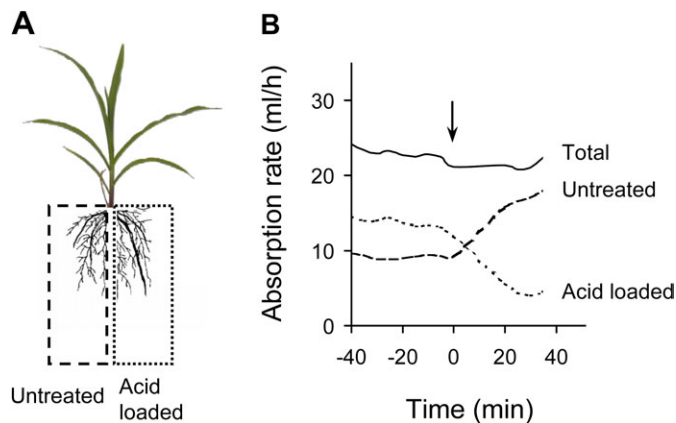


Fig. 1. Effects of a partial acid loading treatment on water absorption rates in maize roots split between two hydroponic compartments. (A) The figure shows how acid loading, an aquaporin inhibiting treatment (Tournaire-Roux *et al.*, 2003; Ehlert *et al.*, 2009), was applied to one half of the root system while the other half was kept in an original Hoagland's solution. (B) Kinetics of water absorption rates by a set of five plants at the six-leaf stage. At time zero (arrow), 20 mM propionic acid was added to one of the two compartments. Absorption rates were measured every minute by independent weighing of the acid loaded and untreated root compartments. Total absorption rate (solid line) is also represented.

same plant (root system) but in deeper soil regions, the overall process resulted in a so-called hydraulic lift. Apart from considerations on plant communities (Jackson *et al.*, 2000), this redistribution of water in the soil via the root system, may be seen, from a single plant perspective, as the mobilization of deep soil water to favour root survival and nutrient acquisition functions in a drying superficial root horizon. More generally, a spatial control by the plant of local hydraulic resistances and linked water potentials throughout the whole root network can be anticipated as a response to soil heterogeneity or other environmental demands (North and Nobel, 2000; North *et al.*, 2004). Interestingly, the hydraulic properties of tree roots at 18–20 m depth have recently been accessed via caves and aquaporin-mediated diurnal and seasonal changes have been recorded (McElrone *et al.*, 2007).

These examples show that the mutual interactions between root and soil hydraulics, and the heterogeneity of both the soil and the root should deserve closer attention in future research on plant responses to drought. As many physiological studies, including ours, have relied on plants growing in aeroponic or hydroponic conditions or in pots (with the soil considered as a homogeneous substrate), the description of water potentials at the root–soil interface will be crucial (Xu *et al.*, 1995; van der Ploeg *et al.*, 2008). The modelling of water uptake in a soil–root system has also provided convincing explanations on how a front of water uptake can propagate during soil drying and how this process is influenced by root architecture and soil properties (Doussan *et al.*, 2006). Finally, it is noted that the most convincing evidence for a role of aquaporins during water stress does not concern the primary response of the plant to drought but its growth recovery performance during rewetting (Martre *et al.*, 2002; Siefritz *et al.*, 2002; Parent *et al.*, 2009). In this context, preservation of root functionality against excessive soil drying pending its rewetting is certainly facilitated by the down-regulation of L_{p_r} . More attention should be brought on these processes.

Root hydraulics and ion relations

As alluded to above, the mutual interactions between solute and water uptake also play a central role in root physiology and can offer another interesting angle to address the significance of root hydraulics. In a general sense, transpiration-induced water flow represents a significant dragging force for solute movement in the soil and the plant whereas solute pumping by the root creates an osmotic force for water uptake.

More specifically, solute diffusion can be limiting in many soil substrates and a vigorous uptake of nutrients by the plant can create a significant nutrient depletion in the soil adjacent to the root absorption zone. The local enhancement of L_{p_r} by nutrients could therefore represent a mechanism for adaptation to heterogeneous soils. It may favour water uptake and, consequently, nutrient drag in those

patches that are the richest in nutrients (Gorska *et al.*, 2008). The converse effects of nutrient deprivation that results in L_{p_r} inhibition may be interpreted in a more global frame. Nutrient deprivation usually enhances root growth to maintain overall nutrient uptake and shoot growth (López-Bucio *et al.*, 2003). Considering that whole root conductance L_0 represents the most relevant root parameter with respect to shoot demand, it is conceivable that the starvation-induced increase in root surface is simply compensated by a decrease in L_{p_r} to adjust L_0 to constant shoot demand. In these respects, the regulation of L_{p_r} by nutrients may reflect the general coupling between root hydraulics and shoot growth that is discussed in the next section.

By comparison to its up-regulation by nutrients, the inhibition of L_{p_r} by soil salinity may reflect a mirror strategy of the plant, to prevent salt drag in contaminated soil areas, and subsequently, in root tissues. It is noted, however, that this model implies that salt is acting locally and not systemically, a point that will have to be explored in split root experiments. Also, it is now well established that most of the short-term effects of salt on L_{p_r} are mediated by an inhibition of the membrane (aquaporin) path (Martinez-Ballesta *et al.*, 2003; Boursiac *et al.*, 2005). This path is, by contrast to the apoplastic path, highly selective for water. A paradoxical effect is therefore that salinity, by favouring compensating flows through the apoplastic path, will decrease the barrier efficiency of root tissues against ion inflow. To reconcile this with the need, for other reasons, of a marked L_{p_r} inhibition (see hydraulic signalling), the root may display differential spatial regulation, with no inhibition of cell hydraulic conductivity (or even a stimulation) in the outer cell layers (epidermis, cortex) whereas aquaporins would be strongly inhibited in the inner tissues (stele). We have recently obtained data along this line in the *Arabidopsis* root (M Sutka *et al.*, unpublished data).

Root anoxia often occurs as a consequence of soil flooding. The resulting decrease in L_{p_r} observed in certain plant species can be such that a somewhat paradoxical water deprivation (wilting) is induced in shoots (Else *et al.*, 2001). The tight coupling of aquaporin closure to the drop in cell energy (one of the earliest consequences of oxygen deprivation) and to the subsequent intracellular acidosis suggests, however, that rapid adjustments in tissue hydraulics are critically needed during the early stages of the anoxic stress. A massive inflow of water in oxygen-deprived (flooded) roots could induce a rapid dilution of the apoplastic spaces and xylem sap. We believe that, as cell ATP is required for energizing solute pumping and export into the xylem vessels, such an inflow of water could be particularly detrimental in plants with a reduced capacity for ion pumping and concentration. Holbrook and Zwieniecki (2003) have proposed an alternative interpretation. Anoxia-induced aquaporin down-regulation may prevent the transport of the ethylene precursor, ACC, away from the root, thereby favouring the local accumulation of ethylene to trigger the differentiation of root aerenchymas. A counter-acting effect of ethylene on the anoxia-induced drop in

L_{p_r} (Kamaluddin and Zwiazek, 2002) may add a control loop to the proposed mechanism. Finally, the L_{p_r} of wheat roots was not changed under a short-term hypoxic treatment but showed an overshoot upon subsequent aeration, possibly to facilitate the recovery of root growth and nutrient uptake (Bramley *et al.*, 2010).

Root-to-shoot interactions

Root conductance and the transpiration stream

A typical example of the complex interactions between plant hydraulics and transpiration can be seen in the diurnal variations of root water uptake and transpiration. Here, the enhancement of L_{p_r} during the day (Henzler *et al.*, 1999; Tsuda and Tyree, 2000; Vandeleur *et al.*, 2009) can be interpreted as a means for preventing a drop of water potential in inner leaf tissues under conditions of strong transpiration (Tsuda and Tyree, 2000). Interestingly, guard cell movements depend on the counterpressure and tensions exerted by adjacent epidermal cells (Franks and Farquhar, 2007). The water status (turgor) of these cells may therefore represent a major integration point of root and shoot hydraulics and stomatal regulation. Christmann *et al.* (2007) also showed that the perception by the roots of a drying soil is transduced to the shoot as an hydraulic signal which primarily decreases leaf cell turgor. This change triggers ABA production in leaves and subsequent stomatal closure (Christmann *et al.*, 2007). A drought-induced drop in L_{p_r} may further amplify this root-to-shoot signalling. This enhanced soil–root–shoot communication finally leads to reduced plant transpiration, thereby preventing a too rapid soil deprivation.

Isohydic and anisohydic plants differ in how tightly they regulate leaf water potential and transpiration under changing air or soil humidity. Stomatal closure and reduced transpiration in response to soil drying is the main mechanism in isohydic plants to prevent leaf water potential from falling to detrimental levels. Several recent reports have shown how elevated plant hydraulic conductance and/or aquaporin activity provide anisohydic plants with the ability to maintain high transpiration and growth under water-limiting conditions (Franks *et al.*, 2007; Sade *et al.*, 2008; Vandeleur *et al.*, 2009). In grapevine, a drought-tolerant cultivar showed, even under water shortage, a marked up-regulation of L_0 at midday, to sustain transpiration and growth in adverse conditions (Vandeleur *et al.*, 2009).

It has already been mentioned that certain physiological contexts, such as anoxia, point to situations where the root hydraulics and stomatal regulation are uncoupled, thereby inducing leaf wilting. Exposure of roots to cold also reduces L_{p_r} (Lee *et al.*, 2004) and can result in a marked water stress in leaves. Although paradoxical, these situations may reflect the need for efficient hydraulic signals coming from the soil to adjust leaf function (Bramley *et al.*, 2010), with respect to transpiration (this paragraph) or leaf growth (see below).

Root hydraulics and shoot growth

Our groups recently investigated the impact of dynamic, aquaporin-mediated changes of L_{p_r} on whole maize plants (Ehlert *et al.*, 2009). For this, L_{p_r} was manipulated using four independent treatments that had previously been characterized as inhibiting aquaporins; acid load at pH 6.0 and pH 5.0, H_2O_2 , and anoxia. The treatments were applied to transpiring plants grown in hydroponics and the effects on leaf growth, leaf cell turgor, water potential, and water flux through the plant were investigated in parallel. Cell turgor measured in the elongating zone of leaves decreased synchronously with L_{p_r} , and leaf elongation rate closely followed these changes across all treatments with a dose-dependent response. These data indicate that stimulus-induced changes in root water transport induce a drop in leaf cell water potential (turgor), which in turn result in an arrest of cell growth. This control of leaf growth through regulation of root aquaporins is very efficient as it occurs in conditions where the transpiration flow is not even altered by a reduced L_{p_r} . It provides another example whereby root hydraulics controls shoot functions.

In some recent work (M Sutka *et al.*, unpublished data), the root water transport properties of a set of 13 natural *Arabidopsis thaliana* accessions were characterized. A significant variability was observed in several of their hydraulic parameters including L_0 . Taking this as an indicator of the whole root water uptake capacity, it was investigated how L_0 could reflect functional links between the root and aerial parts. This parameter was positively correlated to the transpiration rate of plants, as deduced from overall leaf area and stomatal conductance. A strong correlation between root or whole plant hydraulic conductance and transpiration has already been reported in other species including sugarcane, *Eucalyptus*, and grapevine (Meinzer and Grantz, 1990; Franks *et al.*, 2007; Vandeleur *et al.*, 2009). In *Arabidopsis*, this correlation was moderate ($R=0.60$), however, suggesting that under strong transpirational demand, root uptake may not be a major determining factor of the soil-to-atmosphere water flow. By contrast, a stronger linkage of L_0 to organ dry weight (DW) was found, a parameter that reflects their integrated growth. As L_0 is the product of L_{p_r} by the root surface, a link to root DW ($R=0.53$) is easily explainable (Fig. 2). Since the shoot-to-root ratio is a fairly conserved parameter within species, it was no surprise to observe, in addition, a correlation between L_0 and shoot DW. However, it was found that L_0 was more tightly linked to the DW of leaves ($R=0.66$) than to that of roots (Fig. 2). Furthermore, the correlation was enhanced when considering the DW of all aerial parts including floral stems ($R=0.86$). As this organ poorly contributes to transpiration, the latter correlation rather points to a strong link between L_0 and integrated carbon fixation in shoots. The data in *Arabidopsis* accessions therefore suggest that optimized water transport could significantly facilitate the overall growth process, even in the absence or at low transpiration. In these conditions, the root hydraulics would of course contribute to a non-limiting water uptake in expanding tissues (cell

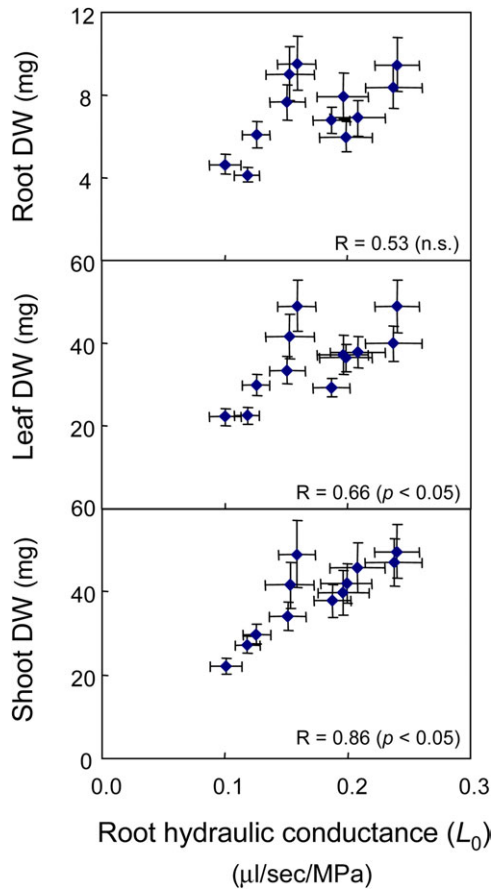


Fig. 2. Relation of root hydraulic conductance (L_0) to organ dry weight (DW) in natural accessions of *Arabidopsis thaliana*. Data were obtained on a set of 13 accessions including the nested core collection of McKhann *et al.* (2004) (M Sutka *et al.*, unpublished data). Plants were grown in hydroponic culture and their L_0 was measured by a pressure chamber technique as described by Boursiac *et al.* (2005). The plots show mean L_0 and mean organ DW values calculated from measurements on $n=22-30$ individual plants of each of the 13 accessions. Spearman's rank correlation coefficients (R) and their statistical significance (p) were determined using STATISTICA software.

expansion). It may also optimize solute uptake from the soil solution. Genetic work in *Arabidopsis* has shown how a specific aquaporin isoform can facilitate osmotic water transport in the root and the coupled loading of water and solutes in xylem vessels (Javot *et al.*, 2003). Optimized root hydraulics may also favour leaf water potential equilibration during the night and enhance the efficiency of carbon fixation at dawn. A study in three rice genotypes has also shown a strong correlation between L_0 and shoot DW, specifically under reduced soil water availability, suggesting that root water uptake is particularly limiting for shoot growth under water-saving conditions (Matsuo *et al.*, 2009).

Conclusion

This paper indicates how the dynamics of root hydraulics contributes to many integrated plant nutritional and growth

functions. Root hydraulics determines water uptake intensities but also water potential gradients within the plant. These two features can be equally important in determining the plant water and nutrient status. It is also shown how the heterogeneity of soil composition and of root hydraulic properties feed each other and play critical roles in the integrated root functions. These aspects will deserve greater attention in future studies. Another important challenge will be to integrate root hydraulics within the mutual interactions of roots and shoots. The combination of aquaporin genetics with integrated physiology and modelling will surely provide critical insights into these questions.

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