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Plant Hydraulic Conductivity: The Aquaporins Contribution

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1. Introduction

In the soil-plant-atmosphere continuum the major resistance to water flux is the leaf-atmosphere interface which determine the rate of transpiration for a specific evaporative demand. In this scenario, the hydraulic resistance of the different plant tissues is minor; however, the hydraulic conductivity of the whole plant is subjected to a tight physiological regulation in which the aquaporins role may result fundamental. The expression of a large number of aquaporins occurs predominantly in roots and different experimental procedures have demonstrated that aquaporins activity is linked to the hydraulics of some species during abiotic stress. However, the plants roots hydraulic properties also depend on the morphology and anatomy of roots and the length of the absorbing region in addition to the influence of aquaporins. These features change during the plant development and in response to environmental stimuli by altering the hydraulic conductivity of the root. To fully understand root system hydraulics and the contribution of native aquaporins, comprehensive studies at different scales are required. In this chapter the definitions used to describe the plant hydraulic resistances are mentioned and the influence of the root anatomy and morphology on hydraulic conductivity is reviewed. Also, the variations in the hydraulic resistances under different abiotic stresses and distinct environmental conditions have been explored. Finally, the different properties and characteristics among various measuring methods are reviewed.

2. Hydraulic resistances: the physiological significance

The water pass from soil though plant to atmosphere has been classically described as a system of hydraulic resistors arranged in series (van den Honert, 1948). However, plants can vary this resistance (and conductance) of the pathways to maintain the water balance of the shoot (Steudle, 2000). When water exists in the vapour phase, the greatest resistance is the stomatal aperture. However, in the liquid phase, the root system constitutes a highly significant and important resistance to overall flow of water in the plant (Steudle, 2000).

A common error in plant water relations is the interchangeable use of hydraulic conductance and conductivity although both parameters are related. Hydraulic conductance is a measure of the ability of an entity to conduct water, independent of the specific entity's dimensions, whereas hydraulic conductivity is a property of an entity with specified dimensions, usually surface area. Conductance or conductivity may be normalized to various dimensions of the particular organ or system relevant to the flow-path, thus conductance of the root system may be normalized to root length or root weight (Tyree et al., 2002). When water transport across a surface is considered (a cell or a root) the concept is expressed by surface area to give what is also termed hydraulic conductivity (Lp, m s^{-1} MPa^{-1}). Conductivity of a stem segment or petiole can be normalized to xylem cross sectional area of a stem segment. Leaf hydraulic conductivity is generally measured as the flux (mmol s^{-1}) divided by the gradient in water potential, $\Delta\Psi$ (MPa), and leaf surface area to give units of mmol m^{-2} s^{-1} MPa^{-1} (Sack & Holbrook, 2006).

Root hydraulic conductivity (Lp_r), is one of the major parameters reflecting root water uptake ability. It has a close correlation with plant water relations under both normal and stressed conditions. The root ability to respond rapidly to fluctuating conditions suggests that Lp_r may participate in plant adaptation to diverse environments (Steudle, 2000). The study of root water uptake has been made progress recently from the anatomical structure of the root to molecular level, i.e., aquaporins activity (Steudle, 2000; 2001). Aquaporins are transmembrane proteins that belong to the Mayor Intrinsic Proteins (MIP), a large family of water channel proteins located in plasma and intracellular membranes and are the main determinants of water flow across plant cells and tissues. Aquaporins can be divided into different subfamilies depending on the sequence homology and subcellular localization, the plasma membrane proteins (PIP, with two phylogenic subgroups PIP1 and PIP2), the tonoplast intrinsic proteins (TIP) the nodulin- 26–like intrinsic membrane proteins (NIPs) and the small basic intrinsic proteins (SIPs) (Javot et al., 2003; Maurel et al., 2008).

The dynamic changes in Lp_r in response to chemical or environmental stimuli may result from modifications of aquaporin abundance or activity (Carvajal et al., 1996; Tournaire-Roux et al., 2003; Boursiac et al., 2005). However, due to the high plasticity of plant root systems both in architecture and metabolism (Liang et al., 1997; Joslin et al., 2000; Linkohr et al., 2002; López-Bucio et al., 2003), and the different properties among various measuring methods and experimental conditions, the root hydraulic conductivity could be highly variable even for the same plant.

Also, leaves contribute to a substantial part of the hydraulic resistance in whole plants (Sack et al., 2003; Sack & Holbrook 2006). Leaf hydraulic conductance may also be linked to transpiration efficiency through regulation of water transport by aquaporins and effects on mesophyll cell water status (Zwieniecki et al., 2007). In fact, ABA (abcisic acid) controls aquaporin PIP levels in the leaf (Morillon & Chrispeels, 2001; Aroca, 2006; Lian et al., 2006; Parent et al., 2009), thereby contributing to the leaf hydraulic conductivity (Morillon & Chrispeels 2001). However, this is not always the case and it has been reported that an antisense inhibition of PIP1 and PIP2 expression did not affect the leaf hydraulic conductance in *Arabidopsis* (Martre et al., 2002).

3. The root anatomy influence on the hydraulic conductivity

In the radial pathway, the water absorbed by the roots has to pass through living tissue, through the walls of the root before reaching the xylem vessels. In the axial plane, the flow

of water occurs along the xylem vessels and tracheids. The relationship between radial and axial resistances determines the resistance of the whole root and distribution of water uptake (Zwieniecki et al., 2003). The composite transport model of water proposed in the roots (Steudle & Frensch, 1996; Steudle & Peterson, 1998) accounts for variable contributions of transmembrane (where aquaporins may exert a control) and apoplastic (independent of aquaporin activity) pathways to the overall root water uptake, depending on the nature and the intensity of the driving force. The model explains why hydrostatic gradients may result in higher root hydraulic conductivity (Lp_r) than for osmotic gradients (Steudle, 2000). However, higher root Lp_r for hydrostatic than for osmotic gradients is not always observed (Bramley et al., 2007b). For example, Lpc of epidermal and cortical cells was much greater than Lpr in *Hordeum distichon* and *Phaseolus coccineus* roots, indicating that water flow mainly via the cell-to-cell pathway (Steudle & Brinckmann, 1989). By contrast, analogous measurements on maize (*Zea mays*) roots revealed a predominantly apoplastic flow (Steudle et al., 1987). Comparing the measured values of Lp_r and Lp_c for each cortical cell layer indicated that radial water flow through wheat (*Triticum aestivum*) roots occurs by a similar contribution of the parallel pathways, but radial water flow in the roots of narrow-leafed lupin (*Lupinus angustifolius*) and yellow lupin (*Lupinu luteus*) appears to be predominantly apoplastic (Bramley, 2006).

In addition, the dynamics of root permeability to water has been also associated with the anatomical and morphological features (Kramer, 1983; Moreshet & Huck, 1991). In cereal roots, a maximum of water absorption in the region of less than 100 mm from the root apex has been observed (Sanderson, 1983) since the water flow resistance is higher in both the radial and the axial pathway in the root zones where there is a developed xylem (Steudle, 2001). Also, the Lp_r of wheat roots decreased with the distance from the root tip, indicating that water absorption occurs preferentially in the apical region (Bramley, 2006).

Rieger and Litvin (1999) found that the root diameter was negatively correlated with Lp_r in five species and that drought stimulated the suberisation and other anatomical changes that reduced the Lp_r. Thus, the apoplastic pathway can be inhibited by the presence of Casparian bands, which are deposits of suberin or lignin in the cell wall (Steudle, 2000). Casparian bands occur in radial and transverse walls of the endodermis and exodermis (Steudle & Peterson, 1998). Hydraulic conductivity uses to decline with root age which is likely due to suberization and loss of the cortex reducing surface area available for water uptake (Wells & Eissenstat, 2002). Frequently, suberized layers may assist in reducing water loss to soil during water deficits. Huang and Eissenstat (2000) determined that structural differences in the radial pathway were the main factors that determined the Lp_r in the roots of citrus rootstocks. In maize plants the development of an exodermis in the roots reduced the radial hydraulic conductivity (Hose et al, 2000; Zimmermann et al, 2000). By contrast, Steudle et al. (1993) demonstrated that the endodermis of young maize roots did not affect the Lp_r. In a similar way, Barrowclough et al. (2000) found that in the roots of onion plants (*Allium cepa*), the highest values of radial hydraulic conductivity were correlated with the presence of exodermis. Thus, the anatomical changes are slow and depend on the plant growth and the genotype, and can act as a survival strategy to reduce long-term Lp_r when environmental changes are slow.

In addition, depending on the length of the root species the absorption region can change (Kramer, 1983). For example, the wheat root length is two to ten times higher than the lupino plants (Gallardo et al., 1996). However, despite these differences in root length, the roots of eudicotyledon species tend to have a higher specific rate of water uptake than

cereals. Moreover, these higher rates of water absorption appear to be due to greater hydraulic conductivity (Bramley, 2006; Gallardo et al., 1996) as occurred in wheat roots where aquaporin activity increased causing an overshoot in Lp_r (Bramley et al., 2010).

Although it was believed that the relation between root water uptake and Lp_r was due only to differences in axial and radial anatomy (Hamza & Aylmore, 1992a; Gallardo et al, 1996), the discovering of the aquaporins supposed a tight regulation mechanism of water flux. Since a significant proportion of radial flow of water occurs from cell to cell through the cell membrane, Lp_r can be controlled by the activity of aquaporins. Thus, measurements of the radial hydraulic conductivity after removal of tissue layers and the application of mercury have shown variable activity of aquaporins in different regions of *Agave deserti*, where aquaporins were to be active in regions associated with living cells with high metabolic activity (Martre et al., 2001; North et al., 2004). Also, in *Arabidopsis thaliana* roots the relative contribution of the apoplastic pathway increased when aquaporin activity was inhibited by mercury treatment which was reflected in L_0 (Martinez-Ballesta et al., 2003).

Finally, the absorption of water for several or all of the individual roots can contribute to Lp_r of the entire root system (Bramley, 2006). There is also evidence that individual roots are capable of varying its hydraulic conductivity. In several experiments Vysotskaya et al. (2004a, 2004b) removed four of the seminal roots of durum wheat (*Triticum durum*) and an increased Lp_r of the remaining roots was observed maintaining the shoot water supply.

4. Hydraulic conductivity and environmental stress

It is known that roots offer the greatest resistance to water flow and that the hydraulic conductivity of the root (Lp_r), may be affected by diverse forms of abiotic stress. Although the hydraulic conductivity of the tissues could be regulated by changes in the level of specific aquaporins, regulation could also occur by changing the activity of these proteins (Carvajal et al., 2000; Zimmermann et al., 2000). Thus, the ability to increase or decrease the water permeability of a cell seems to justify the enormous effort in expressing large amounts of these proteins (Schäffner, 1998). However, water uptake by roots is a variable process that depends on the structure and anatomy of roots which, in turn, is affected by environmental factors such as drought, temperature and heavy metals (Azaizeh et al., 1992; North and Nobel, 1996; Peyrano et al., 1997; Schreiber et al., 1999).

4.1 Water stress

Some stresses, such as drought, could be perceived by the roots and transduced to the aerial part as a hydraulic signal reducing cell turgor in the leaves (Christmann et al., 2007). This change increases the leaf ABA levels and subsequently induces the stomatal closure. The Lp_r drop due to the water deficit could amplify this root-shoot signal, decreasing finally the plant transpiration rate. It has been found a correlation between Lp_r and the transpiration rate for eucalyptus (Franks et al., 2007) or grapevine (Vanderleur et al., 2004). However, under specific physiological context, stomatal regulation and Lp_r are uncoupled and more research about the root-shoot hydraulic signalling is necessary. Thus, it has been reported than under low evaporative demand the stomatal conductance was not affected by the application of aquaporin inhibitors on roots. Consequently, transpiration was steady and the water potential gradient between the root medium and the xylem at the leaf base was increased and counteracted the Lp_r reduction. However, this chemical manipulation of root hydraulic conductivity caused simultaneous effects on leaf growth rate and on cell turgor in

the growing zone suggesting that turgor and growth are coupled (Ehlert et al., 2009). By contrast, under higher evaporative demand, which induced a dramatic decrease in leaf water potential, Lp_r was reduced to values similar to those observed in maize in field conditions (Tardieu & Simonneau, 1998). Also, previous studies of aspen (*Populus species*) (Wan & Zwiazek, 1999) and pepper (*Capsicum annuum*) (Martinez-Ballesta et al., 2003a) also reported that, on a slightly longer term exposure of the roots to $HgCl_2$ induced a significant decrease in stomatal conductance.

The effects of drought on the root hydraulic conductivity depend on the stress level (Siemens & Zwiazeck, 2004) and plant genotype (Saliendra & Meinzer, 1992). If water uptake becomes limiting, the up-regulation of aquaporins expression could enhance cellular water permeability, increasing root hydraulic conductivity, relieves osmotic pumps, and supports the survival during dry periods (Siefritz et al., 2002).

Gene expression studies in various plant species have shown variable responses of aquaporin isoforms to water stress, with both up- and down-regulation of genes evident (Alexandersson et al., 2005; Jang et al., 2004; Sarda et al., 1999; Suga et al., 2002; Yamada et al., 1997). The down-regulation of PIP gene expression and Lp_r by drought stress may result in reduced membrane water permeability, and may promote cellular water conservation during periods of dehydration stress (Jang et al., 2004). In desert plants, the closure of water channels during drought would help prevent root water loss to a soil that generally has a lower water potential than does the plant (North et al., 2004). In leaves, roots, and twigs of olive (*Olea europaea*), OePIP1;1, OePIP2;1, and OeTIP1;1 were significantly reduced at 3 and 4 weeks after water was withheld (Secchi et al., 2007). Overexpression of AtPIP1b in transgenic tobacco (*Nicotiana tabacum*) caused plants wilting faster when water was withheld (Aharon et al., 2003). In contrast, Siefritz et al. (2002) observed reduced resistance to water stress in antisense tobacco plants with reduced expression of NtAQP1, the homologous aquaporin. Recently, Sade et al. (2009) showed that the tonoplast aquaporin SlTIP2;2, is a key to isohydric to anisohydric behaviour conversion, increasing transpiration under normal growth conditions and limiting the reduction in transpiration under drought and salt stresses. This characteristic attributable to overexpression of the TIP isoform SlTIP2;2 do not appear to exist in many PIP-overexpressing plants.

Effects of drought on root hydraulic conductivity will then have different consequences on whole hydraulic resistance and on leaf water potential depending on species. Isohydric cultivars are those that keep their leaf water potential above a certain threshold regardless of soil water availability or atmospheric water demand. The finding of no variation in transcript level of most important root PIP aquaporins and suberisation implies a lower hydraulic conductance in water deficit conditions. This supports the hypothesis of tight control on stomatal regulation that is typical of isohydric cultivars, which aims to avoid excessively negative xylematic water potential and, therefore, cavitation (Schultz, 2003a; Soar et al., 2006; Vandeleur et al., 2009). Anisohydric cultivars are those in which leaf water potential drops with decreasing soil water availability or increasing atmospheric water demand.

4.2 Salinity

It has been reported that salinity affect negatively to the hydraulic conductivity (Munns & Passioura, 1984; Joly, 1989). Although the reductions in root hydraulic conductivity or hydraulic conductance of salinised plants have been suggested as being due to the hyperosmotic stress and ionic imbalance caused by the high apoplastic concentrations of

Na^+ and Cl^- (Evlagon et al., 1990), it has been suggested that these reductions could be due to changes either in the aquaporins functionality or in the amount of this protein in the plasma membrane (Carvajal et al., 2000).

In any case, the L_0 results for the plant roots cannot be always explained in terms of aquaporins abundance in the plasma membrane, as shown in several reports (López-Pérez et al., 2007; Muries et al., 2011). Thus, in root cells of *Brassica oleracea* plants grown with NaCl, apparent disagreement between L_0 values and PIP protein abundance has been observed (Muries et al., 2011). In these plants the most-important modification in the anatomy of the root was phi thickening, which increased in salinity-stressed plants and could be a physical barrier to apoplastic water transport (López-Pérez et al., 2007). The down-regulation of L_0 under saline conditions and the increased protein amount observed could be interpreted as a mechanism to restore and compensate water uptake by roots. Other explanations for the disagreement between L_0 values and PIP protein abundance under stressing conditions could be differences in the contribution of PIP isoforms to the L_0 values or different PIP localisation along the root axis (Benabdellah et al., 2009) or among cellular membranes (Boursiac et al., 2005; Zelazny et al., 2007). Furthermore, a reduction of the phosphorylation state of PIP proteins could cause the observed reduction in L_0 (Wilder et al., 2008) and this and other post-translational modifications as gating control mechanism may be considered.

4.3 Anoxia

Soil compaction or flooding which restrict oxygen diffusion in the soil, result in root anoxia which, in turn, down-regulates Lp_r in certain plant species. Thus, Zhang & Tyerman (1991) using the cell pressure probe showed a 10-fold decrease in the hydraulic conductivity of root cortical cells of wheat under anoxia conditions. These changes in the root hydraulics largely reflected the variations in the transport properties of root cell membranes. Thus, anoxia may reduce the rate of active pumping of nutrients without affecting the passive permeability of roots. Because of the reduction of root hydraulic conductivity, anaerobic conditions should have great consequences for the supply of the shoot with water and, hence, for the whole plant water status. Aquaporins that are highly expressed in roots and facilitate water transport across membranes tended to be down regulated after a few hours of hypoxia (Bramley et al., 2007b). Also, the closure of aquaporins in membranes decreased the hydraulic conductivity and hence increased the half-time of the rate of water exchange across the cell (Bramley et al., 2010).

In *Arabidopsis* plants, hydraulic conductivity inhibition under anoxia or O_2 deprivation by the gating of aquaporins was related to cytosolic acidosis (Tournaire-Roux et al., 2003). Thus, the closure of the plant plasma membrane aquaporin was triggered by the protonation of a conserved hystidine residue under anoxia conditions (Tournaire-Roux et al., 2003). Similarly, in spinach an acidification of the cytosol due to anoxia, would cause a protonation of His 193 in loop D of SoPIP2;1 thereby closing the channel (Törnroth-Horsefield et al., 2006). Also, it has been characterized two protein kinases phosphorylating Ser 115 and Ser 274 in SoPIP2;1 which optima pH reflects the normal cytosolic pH (Sjövall-Larsen et al., 2006). Thus, inactivation of these kinases due to an acidification of the cytosol would lead to a dephosphorylation of Ser115 and Ser274 of SoPIP2;1 and represent an alternative mechanism for aquaporin closing (Törnroth-Horsefield et al., 2006).

These changes in cytosolic pH and H_2O_2 have recently emerged as cellular signals triggered by various external stimuli and mediating pronounced and rapid changes in Lp_r (Aroca et al., 2005; Lee et al., 2004a; Tournaire-Roux et al., 2003).

4.4 Low temperatures

Also, the root system can respond very quickly to changes produced by low temperatures through the variations in its root hydraulic conductivity (Fennell & Markhart, 1998). Chilling induced water stress in plants and it was initiated by the decreased of 17-23% in the root hydraulic conductance followed by a large decrease in leaf water and turgor potential (Aroca et al., 2001). Thus, the water deficit is caused by a reduction in the root water uptake greater than the leaf transpiration rate during chilling (Aroca et al., 2001). The effect of chilling on the root hydraulic conductivity can be attributed to changes in abundance and/or activity of aquaporins (Aroca et al., 2004; Cochard et al., 2007). Thus, in tulip Azad et al. (2004) identified the temperature as an environmental stimulus that induced phosphorylation or dephosphorilation of aquaporins accompanied by changes in the cells water permeability. Reversible phosphorylation is considered as a potent mechanism for plant aquaporin regulation, during development and in the response of plants to environmental stimuli (Luu & Maurel, 2005).

Aroca et al. (2001) reported that chilling-tolerant maize genotype showed an acclimation of Lp_r and root hydraulic conductance was recovered in chilling-tolerant but not in chilling-sensitive varieties. Lee et al. (2004b) showed that in cucumber (*Cucumis sativus*), a cold sensitive species, a brief exposure to low temperature reduces root pressure, hydraulic conductivity, and active nutrient transport. These authors also postulated that changes in the activity of aquaporins underlie the changes in hydraulic conductivity (Aroca et al., 2005; Lee et al., 2004a). Thus, it was concluded that water permeability of cucumber root cell membranes was related to changes in the activity (open/closed state) of aquaporins that were effectively at low temperature (Lee et al., 2005).

In addition to the aquaporins, increased water viscosity accounted for part of the decrease in the L_0 early during chilling (Matzner & Comstock, 2001). Thus, it has been suggested that it is the result of low-temperature-induced alteration of membrane properties that lowers the hydraulic conductance of the symplastic component of radial root water flux (Sanders & Markhart, 2001).

5. Effect of light intensity on hydraulic conductivity

The plant water status is constantly changed by diurnal variations of light intensity as the stoma opening to fix CO_2 is occurring. Therefore, as plants lose substantial amounts of water using the same pathway, they have to develop strategies to optimize the use of water efficiently in response to changes in the light regime, such as variations in hydraulic conductivities of the root (Lp_r) and hydraulic conductance of the leaf (K_{leaf}) (Postaire et al., 2010).

It is well-described that plant leaves respond to light in a short time scale by adjusting leaf hydraulic efficiency. There is also a general consensus that up- or down-regulation of water channels in the plasma membrane of leaf cells plays a central role in the underlying mechanisms. In many plant species it has been reported that the K_{leaf}, can be increased several folds by high irradiance (Nardini et al., 2005, 2010; Lo Gullo et al., 2005; Sack & Holbrook, 2006; Cochard et al., 2007) and can depend on both light duration and intensity (Sellin et al., 2008). Other experiments showed no effect of light conditions on K_{leaf} as it occurs in laurel in laboratory experiments (*Laurus nobilis*) (Cochard *et al.*, 2004) or on K_{lam} (leaf lamina hydraulic conductance) of trembling aspen trees (Voicu et al., 2009). Despite of it, there is current agreement that aquaporin activation and/or expression plays a role in the

underlying mechanisms as the increase in K_{leaf} (Nardini et al., 2005; Voicu et al., 2008). In addition, other studies suggest that this light-induced enhancement involves expression or activation of plasma membrane aquaporins in mesophyll or bundle sheath cells (Tyree et al., 2005; Cochard et al.; 2007, Voicu et al., 2008). This idea is supported by the results obtained by Cochard et al. (2007) who found a very good kinetic correlation between the increase in K_{leaf} and the increase in two walnut aquaporin (*Jr*PIP2,1 and *Jr*PIP2,2) expression during a transition from dark to high light. In the same way, pressure probe measurements revealed that the effect of light on leaf water transport was mediated in part through changes in cell hydraulic conductivity (Lp_c) in midrib parenchyma cells of maize leaves (Kim & Steudle, 2007) where an increasing light intensity increased both Lp_c and aquaporin activity. However higher light intensities (800 and 1800 µmol m^{-2} s^{-1}) dramatically decrease Lp_c probably due to an oxidative gating of aquaporins by ROS (Kim & Steudle, 2009). There should be an optimal light intensity to maximize water flow across leaf cells, but enhanced water flow could be inhibited at a certain light intensity.

Although recent findings showed an inhibition of aquaporin-mediated water transport in tobacco and bur oak leaves exposed to high irradiance (Lee et al., 2009; Voicu et al., 2009), these papers rather indicate that regulation of the aquaporin-mediated water transport processes is more complicated and can not always be explained merely by changes in the transcript level. On the other hand, it has also been shown that exposure of *Arabidopsis* plants to darkness increased the hydraulic conductivity of excised rosettes (K_{ros}) by up to 90% and enhanced the transcript abundance of several PIP genes, including AtPIP1;2 which represent a key component of whole-plant hydraulics (Postaire et al., 2010).

The impact of high irradiance on stem (K_{stem}) and leaf lamina (K_{lam}) hydraulic conductance has also been demonstrated with an increase in K_{stem} (field-grown laurel plants - Nardini et al, 2010; silver birch - Sellin et al., 2010) and in K_{lam} (Voicu et al., 2008) whereas some data suggest that petiole hydraulic conductance (K_{pet}) was unchanged upon illumination (Voicu et al., 2008). The quality of light was also found to have an effect in K_{lam} with a higher increase ranked in descending order as follows, white, blue and green, red and amber light, after a 30-min exposure to high irradiance (Voicu et al., 2008) but not in K_{pet}. Neither of these studies demonstrated a direct involvement of the aquaporins on hydraulic conductance changes.

6. Hydraulic conductivity and biological rhythm

The plant water status is not only challenged by light intensity or darkness but also by diurnal variations (biological rhythm). Since the transport of water and certain other small solutes is facilitated by the function of aquaporins, whose expression and functionality follows the changing demands of the plant physiology during the day or night, it is not surprising that root hydraulic conductivity which is indicative of plant water uptake may also be regulated in a day/night-dependent manner and modified by aquaporin activity (Siefritz et al. 2002). In classic experiments, it was observed that the root hydraulic conductivity declined towards the end of the light period and rose again at the end of the dark period (Parsons & Kramer, 1974). In addition, a diurnal variation of Lp_r was shown in young roots of *Phaseolus coccineus* (Peters & Steudle, 1999) and in excised roots of the legume *Lotus japonicus* grown in aeroponic (mist of nutrient reservoir around the plant roots) or in sand culture (Henzler et al., 1999) where Lp_r was found to vary over a 5-fold range during a day/night cycle, with a maximum around noon. This was correlated to the expression of a

putative PIP1 aquaporin (Henzler et al., 1999) probably due to the conductivity of membranes of endodermal and stellar cells rather than first four cell layers of the cortex where there was no evidence of any diurnal fluctuation.

Diurnal changes in K_{leaf} have been reported in numerous species, but, in most cases, K_{leaf} was increased during the day, concomitantly to a higher transpiration demand (Nardini et al., 2005; Tyree et al., 2005; Sack & Holbrook, 2006; Cochard et al., 2007). A midday depression of K_{leaf} has been reported in the tropical tree species *Simarouba glauca* (Brodribb & Holbrook, 2004), but in this case, it was due to a vulnerability of the vascular system to cavitation rather than aquaporin regulation. Contrary as it occurs in roots, a higher expression of most of the *Zm*PIP genes during the first hours of the light period than at the end of the day or at night (Hachez et al., 2008) was correlated with changes in the membrane water permeability measured using a cell pressure probe in maize leaves (Heinen et al., 2009).

7. Effect of plant nutrition on hydraulic conductivity

An excess or absence of the main elements in plant nutrition can cause disorders in some parameters of water relations such as hydraulic conductance of roots and the activity of aquaporins at the cellular level (Clarkson et al., 2000).

Several works revealed that both N- and P- deficient conditions decreased the Lp_r (Carvajal et al., 1996; Shaw et al., 2002; Shangguan et al., 2005; Fan et al., 2007) and the Lp_c (Radin & Matthews, 1989) in many plant species. This suggests that the lowered root Lp_r of N-, or P- deficient plants may be due to the decreaseds water channel activity or abundance on the plasma membrane (Carvajal et al. 1996, 1998; Clarkson et al., 2000; Shangguan et al., 2005). Such a decrease has also been observed in SO_4^{2-}-deprived barley (*Hordeum vulgare*) roots, where Lp_r decreased to 20% of controls over a 4-d period (Karmoker et al. 1991) On the other hand, Mg^{2+} and K^+ starvation produced a positive effect on L_0 (Cabañero & Carvajal, 2007) and Lp_r (Benlloch-González et al., 2010) respectively. Nevertheless, available data regarding the effect of K^+ deprivation on aquaporin activity are sparse and contradictory. Prolonged deprivation is reported not to lead to any increase in the activity of mercury-sensitive aquaporins in plant roots of several plant species (Maathuis et al., 2003; Cabañero & Carvajal, 2007; Benlloch-Gonzalez, 2009), even though a greater PIP and MIP aquaporin activity has been observed in the early stages of deprivation (Maathuis et al., 2003). This would suggest that transcriptional regulation of aquaporins by low external K^+ at early stages could provide a potential means of preventing osmotic stress during long-term K^+ deprivation.

Concerning nutrient supply or excess, Adler et al. (1996) were among the first to suggest that lower Lp_r under NH^{4+} supply was due to an effect on aquaporin activity. In addition, the excess of nutrients such as of K^+ and Ca^+ produced a toxic effect on L_0 in agreement with aquaporin functionality in pepper plants (*Capsicum annuum* L.) (Cabañero & Carvajal, 2007) while NO_3^- induction of root Lp_r in maize was not correlated with aquaporin expression (Gorska et al., 2008).

8. Different methods for root hydraulic conductivity measurements

Root resistance is an important parameter in determining plant water relations and influencing whole plant responses to multitude of environmental changes and stress

situations, as it accounts for a significant fraction of the entire hydraulic resistance in most plants. Methods for determining the hydraulic conductivity of the entire root system relate the ratio of xylem sap flow, or change in flow, to the difference in water potential, hydrostatic pressure or osmotic potential gradient across the root system, or change of it. These methods include transpirational water flow, osmotically induced flow and hydrostatic pressure-induced flow through the root xylem. Hydrostatic pressure may be applied either to the soil or root medium to induce root exudation (Martínez-Ballesta et al., 2003) or the root xylem through the cut stem surface following excision of the shoot, to induce reverse flow through the roots to the surrounding medium (Frensch & Steudle, 1989; Zhu & Steudle, 1991; Garthwaite et al., 2006; Knipfer et al., 2007).

8.1 Evaporative water flow method

Determination of the root hydraulic conductivity by means of the transpirational water flow method involves the ratio of transpiration to the water potential difference induced across the xylem (root surface to xylem) of the root system. By this method, the measurements are carried out under undisturbed conditions, since the use of transpiration require that the hydraulic pathway is followed by transpiration (Tsuda & Tyree, 2000) without imposed gradients. This method is very practical in the field conditions but its accuracy is limited by the relatively low precision by which the water potential and transpiration can be measured in the field, particularly with large plants. However, under controlled environment conditions with adequate evaporative demand, steady-state transpiration and differences in the osmotic pressure may be readily attained, preventing changes in tissue water content.

8.2 Hydrostatic pressure-induced root exudation method

Measurements of root hydraulic conductivity by pressurising roots are one of the methods most frequently used under laboratory conditions. The entire root system of a detached pant is sealed in a pressure vessel with the cut stem surface exposed to ambient pressure through a seal in the top. Hydrostatic pressure is applied to the root system inducing nutrient solution to flow through the root to the unpressurised cut stem surface (Martinez-Ballesta et al., 2003). The method imposes a unnatural gradient in water potential, and could lead to irreversible changes in the soil-root interface, so that root conductance determined by this method may not accurately reflect the true value under natural conditions, particularly with root systems grown in soil. However, this method, in plants grown in hydroponic solution, the root exudation is more readily attained and more linearly related to applied pressure.

8.3 Natural exudation method

Collecting root exudates under natural root pressure for measuring hydraulic conductance is also widely used (López-Perez et al., 2007). However the flow rate detected by this method hardly represents the natural status of transpiring plants (Emery and Salon, 2002). Using the hydrostatic pressure chamber to force xylem sap out from decapitated plants, it is difficult to know exactly how high the applied pressure should be, because different values of over pressure can result in different xylem water fluxes (Else et al., 1995). In any case, the flow rate is influenced by the inherent hydraulic conductivity of root systems, measured as a conductance. Therefore different values will be obtained, those using the pressurising chamber will be higher as a consequence of pressurizing the roots. In this case, water movement will occur through the apoplast to a greater extent than when the measurements

are obtained by natural exudation. Therefore, the resulting root hydraulic conductance will be higher.

8.4 Root pressure probe method

Root pressure probe (RPP) is one of the most reliable techniques able to measure hydraulic conductivity of plant roots. RPP have been used to measure root pressure and water and solute flows (Steudle, 1993). Other important issues is the ability for separating the axial hydraulic resistance of xylem vessels from that related to flow across the root cylinder and to measure the radial hydraulic resistance of individual root zone (Lee et al., 2004b). In this method, the excised segment of the root or whole root system (excised close to its base) from plants is fixed to pressure probe for continuously recording of the root pressures with the aid of a pressure transducer. Water flow across the root could be induced either by changing the hydrostatic pressure in the probe by moving a metal rod with the aid of a micrometer screw or by exchanging the root medium by a medium containing a test solute of known osmotic pressure (Frensch and Steudle, 1989; Lee et al., 2004b). Transient responses in root pressure allow Lp_r to be calculated from rate constant or half-times of pressure relaxations (Steudle et al., 1987).

Root pressure probe has been used to work out the water and solute permeability of roots. As for some species, the results indicate a considerable cell-to-cell component, whereas in others, the apoplast seemed to be preferred (López-Perez et al., 2007). However, the relative contribution of pathways also depended on the nature of the forces applied. In osmotic experiments, the cell-to-cell path was preferred, whereas in hydrostatic experiments the flow was predominantly in the apoplast. The results obtained with the pressure probe measurements indicated the consistence of the technique since the extended osmometer model in which the osmotic barrier in the root is looked at a composite membrane system.

However, in spite of all these methodologies, the mechanism of water ascent has been the subject of much controversy during years. The development of thermocouple psychrometers and of the pressure chamber technique permitted indirect estimates of the xylem pressure on a large number of species.

A major difficulty with the use of psychormeters approach is the extreme sensitivity of the measurement to temperature fluctuations. For example, a change in temperature of 0.01°C corresponds to a change in water potential of about 0.1 MPa. Thus, psychrometers must be operated under constant temperature conditions. For this reason, the method is used primarily in laboratory settings. Because of its feasibility and its simplicity, the pressure chamber technique is widely used by plant physiologists, but also by farmers to measure plant water stress and schedule irrigation. For many species, hydraulic conductance, as determined with these techniques, typically ranges between −1 and −2MPa. Also, direct measurements of hydraulic conductance have been attempted by the pressure probe. In this case, the pressures that were recorded with this technique were much less negative (in the range of 0 to −0.5MPa) than the values produced by the pressure chamber, although new experiments have recently been conducted with the pressure probe (Wei et al., 1999) and were found to agree with the pressure chamber.

Thus by the pressure probe the hydrostatic pressure of individual cells may be measured directly. However, the primary limitation of this method is that some cells are too small to measure. Furthermore, some cells tend to leak after being stabbed with the capillary, and others plug up the tip of the capillary, thereby preventing valid measurements. However,

technical problems with cavitation limit the measurement of negative pressures by this technique.

9. Conclusion

Root hydraulic conductivity is one of the main parameters that reflect the capacity of the root to uptake water. It confers to the root the ability to respond rapidly to fluctuating conditions suggesting that this parameter may be involved in the plant adaptation to diverse environments. After the aquaporins discovery the dynamic changes in the hydraulic conductivity were attributable to the modifications of the abundance or activity of these water channels. However, root plasticity and its ability to adapt the water uptake to the variable environment is also the consequence of root architecture and metabolism. Thus, the anatomical and morphological features of the roots, such as the diameter or length, the cell layer and its degree of suberisation and the radial and axial water transport pathway have a great influence on the hydraulic conductivity. Thus, the heterogeneity of aquaporins and of root hydraulic properties feed each other and play critical roles in the integrated root functions.

Several abiotic stresses such as drought, salinity, soil compaction or flooding and low temperatures as well as the light intensity, diurnal variations and the nutritional status affect the hydraulic conductivity of the tissues changing their resistance to water flow and where the role of aquaporins may be essential. The combination of aquaporin genetics with integrated plant physiology will provide critical insights into the hyadraulic conductance architecture in response to these stresses.

Regarding hydraulic conductance methodologies the Scholander chamber is the best option for field measurements, however, the validity of the pressure chamber technique has been seriously challenged and new experimental evidences are needed to rehabilitate the technique.

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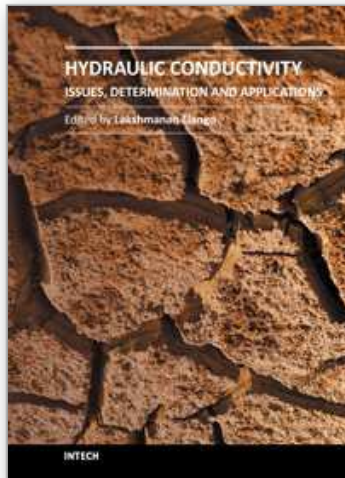
Hydraulic Conductivity - Issues, Determination and Applications

Edited by Prof. Lakshmanan Elango

There are several books on broad aspects of hydrogeology, groundwater hydrology and geohydrology, which do not discuss in detail on the intrigues of hydraulic conductivity elaborately. However, this book on Hydraulic Conductivity presents comprehensive reviews of new measurements and numerical techniques for estimating hydraulic conductivity. This is achieved by the chapters written by various experts in this field of research into a number of clustered themes covering different aspects of hydraulic conductivity. The sections in the book are: Hydraulic conductivity and its importance, Hydraulic conductivity and plant systems, Determination by mathematical and laboratory methods, Determination by field techniques and Modelling and hydraulic conductivity. Each of these sections of the book includes chapters highlighting the salient aspects and most of these chapters explain the facts with the help of some case studies. Thus this book has a good mix of chapters dealing with various and vital aspects of hydraulic conductivity from various authors of different countries.

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