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Water uptake by plant roots: an integration of views

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Abstract

A COMPOSITE TRANSPORT MODEL is presented which explains the variability in the ability of roots to take up water and responses of water uptake to different factors. The model is based on detailed measurements of 'root hydraulics' both at the level of excised roots (root hydraulic conductivity, Lp_r) and root cells (membrane level; cell Lp) using pressure probes and other techniques. The composite transport model integrates apoplastic and cellular components of radial water flow across the root cylinder. It explains why the hydraulic conductivity of roots changes in response to the nature (osmotic vs. hydraulic) and intensity of water flow. The model provides an explanation of the adaptation of plants to conditions of drought and other stresses by allowing for a 'coarse regulation of water uptake' according to the demands from the shoot which is favorable to the plant. Coarse regulation is physical in nature, but strongly depends on root anatomy, e.g. on the existence of apoplastic barriers in the exo- and endodermis. Composite transport is based on the composite structure of roots. A 'fine regulation' results from the activity of water channels (aquaporins) in root cell membranes which is assumed to be under metabolic and other control.

Variability of root hydraulics

Water supplied to the plant by the root contributes to the overall water balance of the shoot. Despite this important function of roots, relatively little is known about the processes that govern or even regulate root water uptake. There is much evidence that the force driving water across roots is usually provided by the tension (negative pressure) created by transpiration from the shoot and extending to root xylem (Steudle, 1995; Tyree, 1997). Hence, the force driving water across the root cylinder is usually a gradient in hydrostatic pressure. However, there are conditions under which the root acts as an osmometer rather than just a hydraulic resistor. They occur, when, in the absence of transpiration, the uptake of nutrient ions into the xylem causes an osmotic water flow and a build up of root pressure. Instead of being dragged up to the shoot by negative pressure, the positive root pressure pushes xylem sap into the shoot under these conditions. Usually the resistance for axial flow along the xylem is much smaller than that for radial flow across the root cylinder (Steudle and Peterson, 1998). For a given plant, both hydraulic resistances are variable for different reasons. Reasons of the variability of radial hydraulic resistance of roots are complex. They are closely related to the complex structure of roots. The phenomenon has been known for a long time (Brewig, 1937; Brouwer, 1954; Fiscus, 1975; Kramer and Boyer, 1995; Passioura, 1988; Steudle, 1989, 1994; Steudle and Frensch, 1996; Steudle and Peterson, 1998). However, no satisfactory model(s) have been presented so far to explain the finding which is crucial for our understanding of plant water relations.

There are changes in root hydraulic conductivity which are due to root development and aging. Moreover, for a given root, the hydraulic conductance (inverse of hydraulic resistance) may vary in response to external (e.g. drought or salinity) or internal factors such as the nutritional state and water status of the plant or the demand for water from shoot caused by transpiration. Mechanisms are poorly understood. For the plasticity of root hydraulics, different reasons have been discussed, i.e.:

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– changes in root morphology, structure and anatomy,
– changes in the transport pattern or mechanism of water flow,
– interactions between water and solute (nutrient) flow, and
– changes in the activity of water channels.

In the following review these factors are briefly discussed. A model is put forward which, at least qualitatively, explains the variability in root hydraulics. The model is quite flexible and allows to integrate different views which have been dsicussed in the past. Some recent findings are summarized which support the model.

Root anatomy

With respect to water permeability, changes in the suberization of roots are most relevant. Suberization of roots increases with age and during stress (drought, high salinity, nutrient deprivation, anoxia, etc.). Young roots suberize when they pass through different stages of development of the endo- and exodermis. During state I, Casparian bands are forming in radial walls of the endodermis. During state II, suberin lamellae are laid down in both radial and tangential walls. Eventually, cell walls are thickened during state III which results in the well-known u-shaped cross section of endodermal cells. It has been shown that the exodermis also develops Casparian bands and that this structure then passes through similar states as the endodermis which includes the formation of passage cells (Peterson and Enstone, 1996). In young maize roots, the formation of a Casparian band in the exodermis did not affect hydraulic conductivity during state I (Peterson et al., 1993; Steudle et al., 1993). However, this may change during later states. For the exodermis, experiments indicated a strong effect on the radial hydraulic conductivity (root Lp_r; Zimmermann and Steudle, 1998). In recent years, considerable information has been collected of how changes in root structure caused by drought, high salinity, anoxia, and nutrient deprivation are reflected into changes of root hydraulic properties (Azaizeh et al., 1992; Birner and Steudle, 1993; Carvajal et al., 1996; Cruz et al., 1992; North and Nobel, 1991; Peyrano et al., 1997; Stavosky and Peterson, 1993). Fairly little is known about the contribution of older thickened roots to overall water uptake. These roots are covered with several layers of suberized cells, e.g. in woody species. Usually, it is thought that, because of suberization, these arrays do not contribute much to overall water uptake. However, this has been questioned by Kramer some time ago (see discussion and literature in Kramer and Boyer, 1995, pp. 184). For technical reasons, it is still difficult to quantify the uptake of different parts of roots or even root zones. Different from the situation in the shoot, much less is known about the 'hydraulic architecture of roots'. This is due to the lack of techniques which would allow to resolve the hydraulic conductivity of root zones in an extensive root system sitting in soil with sufficient accuracy.

On top of these uncertainties, which are largely related to transport properties of the root apoplast, there are open questions with respect water channels (aquaporins) and how they would contribute to the overall water permeability of roots. Water channel activity considerably affects water transport at the cellular (membrane) level (see below; Azaizeh et al., 1992; Frensch et al., 1996; Jones et al., 1983; Steudle and Jeschke, 1983; Steudle et al., 1987; Zhu and Steudle, 1991). For technical reasons, there are, to date, only a few experimental approaches to measure the hydraulic conductivity at the root cell level and to relate this to the overall hydraulic conductivity of the entire organ during different stages of development (Steudle and Jeschke, 1983; Jones et al., 1983; Steudle et al., 1987; Zhu and Steudle, 1991; Azaizeh et al., 1992; Frensch et al., 1996). However, this information is badly needed to work out appropriate models for the water uptake of roots and how this would be controlled or regulated under different conditions. Detailed information on water transport has to be related to root anatomy which can be quite variable. There are differences in root anatomy and structure between species, habitats and growth conditions. When general conclusions are drawn about transport mechanisms and models are worked out, the strong relation between structure and function of roots has to be carefully considered (Steudle and Peterson, 1998).

Transport pattern and mechanisms

Besides other factors, changes in transport mechanism(s) for water which cause changes in the radial water uptake (root hydraulic conductivity, Lp_r), are related to the intensity of water flow and to the nature of forces applied to drive water across the root. The Ohm's law analogy of water flow (van den Honert, 1948) may not hold for roots in all cases. This law

predicts that water flow across a root would linearly increase in proportion to the force driving the flow which is the gradient in water potential between soil and root xylem. One would think that the different components of water potential (hydrostatic and osmotic pressure, matric and gravitational potential) have the same effect on the flow. However, this is not the case. Depending on the species used, there are large differences in root hydraulic conductivity ('root Lp_r') observed either during osmotic (such as during conventional exudation of an excised root) or hydraulic water flow (such as in transpiring plants). Careful investigations have shown that the story is tied up with the question of how water uses the different pathways which are potentially available in roots (see below). Furthermore, the hydraulic resistance of roots usually decreases when the force (flow rate) increases, i.e. there is a non-linear relationship between forces and flows.

In the root cylinder there are three different pathways (Figure 1). The first is the apoplastic path around protoplasts. The second path is the symplastic which is through plasmodesmata. When travelling along this latter path, water stays within the 'cytoplasmic continuum'. Last but not least, we have the transcellular or vacuolar pathway which is across membranes. This latter route is something special for water. It is due to the high permeability of membranes to water. For ions and other solutes present in plant cells, the contribution of this component will be usually negligible. Although there have been attempts to use the pressure clamp-technique to work out symplastic and transcellular components of water flow (Murphy and Smith, 1998), there are, to date, no approaches to separate components in a way which is experimentally simple and straightforward. Therefore, they are summarized as a 'cell-to-cell' or 'protoplastic' component.

In the usual picture of water transport in roots which is dealt with in textbooks, the flow of water across the root cortex is largely apoplastic. This changes at the endodermis because of the Casparian band which interrupts the apoplastic path. There will be a transcellular transport step at the endodermis which is usually thought to rate-limit water transport across young roots. In the stele, the situation will be then similar to that in the cortex.

Detailed measurements of root hydraulics have shown that this simple picture has to be modified. Depending on the conditions, the relative contribution of pathways to the overall uptake or hydraulic conductivity may change substantially. A 'composite transport model of the root' has been established which takes into account the structure of roots (or of other tissue) and is based on irreversible thermodynamics (Figure 2; Steudle, 1989; 1994; 1997; Steudle and Frensch, 1996; Steudle and Peterson, 1998). The model shows that the different pathways may be used with different intensity which then results in the observed plasticity in root hydraulics. Besides the intensity of water flow, the physical nature of driving forces is crucial. In the presence of (hydrostatic) pressure gradients, flow is largely around protoplasts (apoplastic), because this path represents a low hydraulic resistance. The data indicate that there should be some apoplastic flow even across the endodermis, i.e. Casparian bands appear to be somewhat permeable to water (but not to ions) during state I or even later. This results in a high overall hydraulic conductivity of the root (root Lp_r) which is sometimes even larger than that of the plasma membrane of individual root cells. On the other hand, water flow in the presence of osmotic gadients is low as would be the case in the absence of transpiration and during phenomena such as root exudation. Osmotic driving forces only cause a water movement in the presence of membranes. Provided that osmotic gradients applied from outside do not create hydrostatic or matric forces within the root (Zimmermann and Steudle, 1998), an osmotic water flow across the root has to pass many membranes which results in an overall root Lp_r which is much less than that found during hydraulic water flow.

The composite transport model of the root

The composite transport model is based on detailed measurements of hydraulic conductivity and other transport properties (salt permeability and reflection coefficients) which have been obtained both at the level of individual cells and entire roots (see reviews: Steudle, 1989; 1994; 1997; Steudle and Frensch, 1996; Steudle and Peterson, 1998). An important feature of the model is that there are two parallel pathways present which exhibit a quite different 'passive selectivity' as expressed by their reflection coefficients (σ_s). To a first approximation, the cell-to-cell (protoplastic) path is semipermeable, i.e. it exhibits a ${\sigma_s}^{cc}$ of close to unity. The apoplastic path, on the other hand, does not select between water and solutes (nutrient salts and others). The reflection coefficient here (${\sigma_s}^{apo}$) is, therefore, close to zero. The two pathways interact with each other, and the interaction results in phenomena such as a circulation flow of water and a

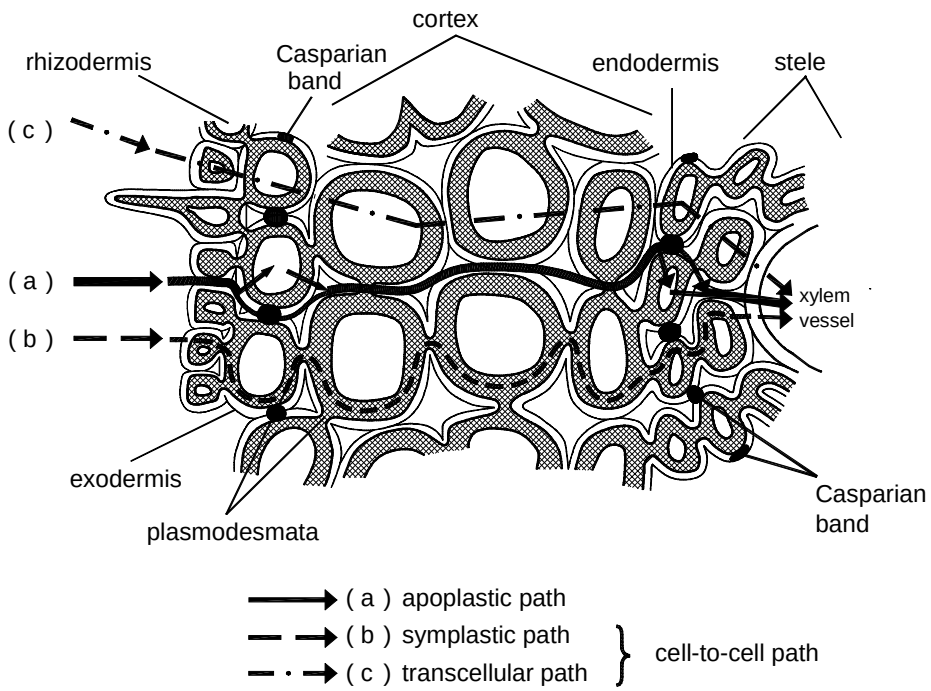

Figure 1. Pathways for the movement of water and solutes in roots. The apoplastic path **(a)** refers to the flow around protoplasts. The symplastic component defines flow from cell to cell via plasmodesmata **(b)**. On the third route **(c)**, water and solutes have to cross cell membranes (two membranes per cell layer; transcellular path). The transcellular path is important for water, but is of minor importance for solutes. For water, pathways **(b)** and **(c)** cannot be separated experimentally to date. Therefore, they are summarized as a cell-to-cell path. It is usually assumed that, in roots, the Casparian bands in the exo- and endodermis completely interrupt apoplastic transport. Here, it is, however, indicated that there may be an apoplastic component of water flow across Casparian bands.

low overall reflection coefficient of the root (as measured). An important consequence of the model is that the hydraulic resistance of roots of transpiring plants will be low, i.e. in the presence hydrostatic pressure gradients. Moreover, the supply from the root is adjusted according to the demands of the shoot. In the absence of a demand, there will be only osmotic gradients present due to the active uptake of solutes by the root. These, however, will cause a much smaller root Lp_r and water flow. The hydraulic resistance of the root will be high. As a consequence, losses of water to a dry or saline soil will be delayed under these conditions. Hence, composite transport provides some kind of a switching between transport models and a 'coarse regulation of water flow' across roots which is favorable for the plant.

The composite transport model readily explains the variability of root hydraulic properties in terms of changes in forces which cause a switching between the pathways used. Along the apoplast, a dependence of the hydraulic conductivity on the nature of the driving force has been discussed as well, to account for some of the changes in the overall root Lp_r. These changes in the hydraulics of the apoplast may be brought about by changes in the water content of cell walls and other things (Steudle and Frensch, 1996). Most interestingly, there are species in which root Lp_r is not as variable as in others. For example, in *Phaseolus coccineus* and barley, the hydraulic and osmotic Lp_r were similar (Table 1). This has been interpreted by a high membrane Lp (in *P. coccineus*) or a rather tight Casparian band (in barley).

Table 1. Root hydraulic conductivity (Lp_r), solute permeability (P_{sr}), and reflection coefficients (σ_{sr}) of roots of **herbaceous (A) and woody (B) species** as determined with the root pressure probe and other techniques. Where available, hydraulic conductivities of root cell membranes (cell Lp) are given for comparison. Because of the high cell Lp, there are no differences between osmotic and hydraulic water flow (Lp_r) in barley and *Phaseolus coccineus*. For maize and *Phaseolus vulgaris*, there are large differences. Differences between osmotic and hydraulic water flow are much larger for roots of trees than for those of herbs. Tree root Lp_r is, on average, smaller by an order of magnitude than that of herbaceous plants. Values of root σ_{sr} are significantly lower than unity for solutes for which cell membranes exhibit a σ_s of virtually unity. σ_{sr} values of tree roots are substantially smaller than those of roots of herbs. The findings are explained by the composite transport model of the root (see text). (n.m. = not measurable)

Species	Root $Lp_r \cdot 10^8$ ($m\ s^{-1}\ MPa^{-1}$)		Root permeability, $P_{sr}\ 10^9$ ($m\ s^{-1}$)	Root reflection coefficient, σ_{sr} (1)		Techniques	Ref.
	hydraulic	osmotic					
A. Herbaceous plants							
Hordeum distichon, primary root	0.3 – 4.3 *Cell Lp: 12*	0.3 – 4.3	–	mannitol:	≈ 0.5	Cell and root pressure probe	(a)
Zea mays, primary root	1–46 *Cell Lp: 24*	0.1–5	sucrose: 3.0 NaCl: 6–14	mannitol: sucrose: NaCl, KCl:	04.–0.7 0.54 0.5–0.6	Cell and root pressure probe	(b) to (e)
Zea mays, root system	21	2.2	—	nutrients:	0.85	Stop-flow technique and osmotic flow	(f) and (g)
Allium cepa, primary root	14	0.02–2	$NaNO_3$: 0.7	KCl, mannitol, and NH_4NO_3:	$NaNO_3$, 0.35–0.88	Root pressure probe	(h) to (j)
Phaseolus coccineus, *coccineus*, primary root	2–8 *Cell Lp: 30-470*	3–7	mannitol; 0.15 NaCl:0.21 KCl: 0.7–0.9	mannitol: NaCl: KCl:	0.68 0.59 0.43–0.54		
Phaseolus vulgaris, root system	30	0.56	nutrients: 1.3	nutrients:	0.98	pressure chamber and osmotic flow	(f) and (k)
B. Woody plants							
Picea abies, root system	6.4	0.017	n.m.	Na_2SO_4, K_2SO_4, 0.18–0.28	$Ca(NO_3)_2$:		
Quercus robur, root system	0.5–4.8	0.003-0.062	n.m.	mannitol: NaCl, KCl:	0.19–0.43 0.12–0.35	Root pressure probe	(l) to (n)
Fagus sylvatica, root system	0.35–1.6	0.022–0.11	n.m.	mannitol: KCl: NaCl:	0.29–0.82 0.22–0.55 0.32–0.64		

(a) Steudle and Jeschke, 1983; (b) Steudle et al. 1987; (c) Steudle and Frensch 1989; (d) Zhu and Steudle, 1991; (e) Peterson et al., 1993; (f) Newman, 1973; (g) Miller, 1985; (h) Melchior and Steudle, 1993; (i) Melchior and Steudle, (1995); (j) Steudle and Brinckmann 1989; (k) Fiscus, 1986; (l) Rüdinger et al., 1994; (m) Steudle and Meshcheryakov, 1996; (n) Steudle and Heydt, 1997.

Composite transport model of root

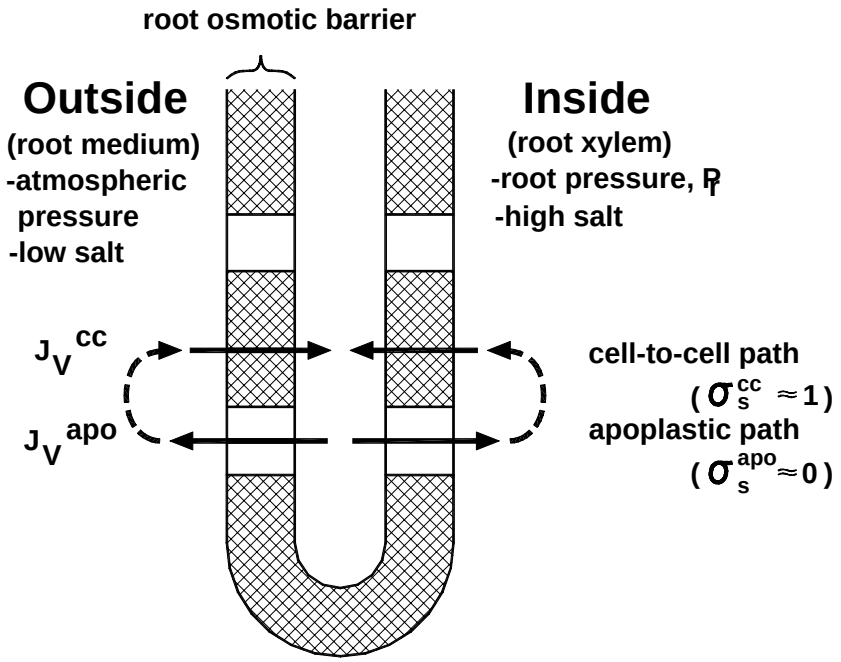

Figure 2. Composite transport model of root (schematical). The root osmotic barrier is comprised of cells (protoplasts) and the apoplast. The apoplastic path may be interrupted by Casparian bands in the endo- and exodermis (not shown for sake of simplicity). Water and solutes move along the two parallel pathways (cell-to-cell and apoplastic route). The cell-to-cell path has a high selectivity (reflection coefficient, $\sigma_s{}^{cc} \approx 1$), and the apoplastic path a very low selectivity ($\sigma_s{}^{apo} \approx 0$) for solutes. At low rates of transpiration, this results in a circulation flow of water in the root and in a low overall root σ_{sr} (as found experimentally). The model explains variable root hydraulic conductivity which depends on the nature of the driving force and other things. For further explanation, see text.

Interactions between water and solute flow

As solutes (nutrients) move across the root cylinder, osmotic concentrations within the apoplastic and protoplastic compartments change. This, in turn, causes a redistribution of water between pathways. The composite transport model accounts for these interactions. In the model, the diffusion along the apoplast is taken into account. Along the cell-to-cell path, the diffusive transport of solutes will be usually negligible because of the low membrane permeability of solutes (nutrients). Active transport may be important at low rates of transpiration. This may be accounted for in the model provided that the rates of uptake by cells in different layers is known.

Another important point which relates to water/solute interactions, is the fact that water uptake into the root xylem reduces the osmotic concentration of xylem sap. In turn, this modifies the force driving water uptake. As water uptake increases during transpiration, the concentration of xylem sap is reduced at a constant rate of active uptake of nutrients. At sufficiently large rates of uptake, the osmotic driving force will vanish. Fiscus (1975) analyzed this 'dilution effect' quantitatively. He found that the effect may account for some of the 'apparent' variability of root Lp_r reported in the older literature. This may be true. However, recent studies with excised root systems of maize have shown that most of the differences between osmotic and hydraulic Lp_r remain even when the dilution effect is accounted for (Zimmermann and Steudle, 1998). Thus, there are inherent differences in root Lp_r which are related to changes in the mechanisms of flow. As pointed out, the differences are physiologically important, namely, during the adaptation of plants to water stress.

Role of water channels (aquaporins) in roots: is there a fine regulation of water flow?

It has been shown that water channels or aquaporins contribute to most of the hydraulic conductivity (water permeability) of plant cell membranes (Chrispeels and Maurel, 1994; Hertel and Steudle, 1997; Maurel, 1997; Schäffner, 1998; Steudle, 1997; Steudle and Henzler, 1995; Schütz and Tyerman, 1997; Tyerman et al., 1999). Water channels are transport proteins of a molecular weight of about 30kDa. They belong to a highly conserved group of proteins called membrane integral proteins (MIPs). MIPs are fairly hydrophobic. Common to all MIPs are six transmembrane domains which span the membrane and two smaller hydrophobic loops on either side containing the asparagine-proline-alanine (NPA) motif (Park and Saier, 1996; Reizer et al. 1993). The NPA motif is thought to be the part of the pore region creating the selectivity for water. The entire structure resembles an hour glass (Jung et al., 1994; Walz et al., 1995). The aquaporin AQP1(CHIP28) forms water channels in the plasma membrane of red cells and epithelia (Nielson and Agre, 1995; Preston et al., 1992). It has been crystallized and structurally resolved (Jap and Li, 1995; Cheng et al., 1997; Walz et al., 1997). AQP1 forms tetramers but each monomer is thought to facilitate water flow (Verkman et al., 1996). The first MIP from plants was cloned and functionally expressed in 1993 (γ-TIP; Maurel et al., 1993). This has renewed interest in the biophysics of plant water (Chrispeels and Maurel 1994; Maurel, 1997; Schäffner, 1998; Steudle and Henzler, 1995). It has been shown that, although water channels are selective for water, there may be some slippage of small organic molecules (Henzler and Steudle, 1995; Hertel and Steudle, 1997). Mercurials such as mercuric chloride ($HgCl_2$) have been used to reversibly block the channel function. This has been demonstrated either in frog oocytes, where channel protein was expressed, or in *Chara* internodes (Chrispeels and Maurel, 1994; Schütz and Tyerman, 1997; Steudle and Henzler, 1995). During tissue transport such as in roots, water channel activity should affect root Lp_r and, hence water uptake. However, from what has been discussed so far, this should depend on the flow model, i.e. on the actual contribution of the cell-to-cell (protoplastic) path to overall water flow (root Lp_r).

It is interesting that water channel activity may be controlled by metabolism (e.g. by a phophorylation of aquaporins; Johansson et al., 1996) or may be triggered by environmental factors (Steudle and Henzler, 1995). In pea, water shortage increased the expression of water channels (Guerrero et al., 1990). In corn roots, high salinity reduced the permeability to water of both root cells and (to a lesser extent) whole roots (Azaizeh and Steudle, 1991; Azaizeh et al., 1992). Carvajal et al. (1996) have shown that depriving wheat plants of nutrients also decreased root Lp_r, apparently by affecting the activity of water channels. These findings are in line with the observation that treating roots with mercurials reduced root Lp_r reversibly (Maggio and Joly, 1995). At the level of individual internodes of *Chara*, the effect has been documented in great detail (Henzler and Steudle, 1995; Schÿtz and Tyerman, 1997; Steudle and Henzler, 1995; Tazawa et al., 1996; Wayne and Tazawa, 1990) In these experiments, water channel activity has been titrated with mercuric chloride or p-chloromercuriphenylsuolfonic acid (p-CMBS). Similarly, high external concentrations of permeating solutes have been employed to cause a closure of water channels in *Chara* (Steudle and Henzler, 1995). Higher plant cells have been also used in these latter studies which were performed with the aid of the cell pressure probe (Steudle, 1993). The results demonstrated that water and the small uncharged solutes used different pathways to cross the plama membrane, as postulated in the presence of selective pores for water which allow for most of the water flow. However, the quantitative treatment of interactions between water and solute flows showed that there was some slippage of the small test solutes across water channels which caused some drag of solvent (water). To date, there are no equivalent experiments with cells of plant tissue such as with root cortical cells. One would need to measure cell Lp in the presence and absence of functioning channels as well as the overall root Lp_r and compare the results. Changes in the expression of water channels in different root tissue would have to be demonstrated as well (Schäffner, 1998). These experiments are underway.

Fine regulation vs. coarse regulation

So far, the results with roots indicate that there is a regulation of water uptake along the cell-to-cell passage, namely, in older suberized roots where the apoplastic path is blocked. So, water channels may be looked at as a tool to provide some ‘fine regulation of water uptake’ in tissues when the apoplastic path cannot be used (Steudle, 1997; Steudle and Peterson,

1998). Regulation along the cell-to-cell path may be affected by external factors such as high salinity, nutrient deprivation, anoxia, and temperature (Azaizeh and Steudle, 1991; Azaizeh et al., 1992; Birner and Steudle, 1993; Carvajal et al., 1996; Henzler et al., 1998; Hertel and Steudle, 1997). It may be mediated by a phosphorylation of the transport proteins (Johansson et al., 1996). Future work has to show if this is true. This work has to imply both the *in situ* characterization of transport proteins and the measurement of its function at the cell and root levels. In terms of root physiology it would be most important to find out the mechanisms which trigger the opening and closing of water channels, i.e. the mechanisms of the gating of water channels (Tyerman et al., 1999).

Experimental techniques

At the level of individual root cells, water transport (hydraulic conductivity, Lp) has been measured using the cell pressure probe (Steudle, 1993; Steudle et al., 1987; Zhu and Steudle, 1991; Figure 3). The tip of the probe (diameter: 2 to 7 μm) was introduced into individual cells in different layers of the root which then allowed the monitoring of cell turgor. Cell Lp was measured after manipulating the equilibrium turgor to produce a water flow across the membrane which was monitored as a 'pressure relaxation'. The half-time of the process is a measure of Lp. In the same, or in a separate experiment, the root pressure probe has been employed to measure the overall hydraulic conductivity of roots (Steudle, 1993; Steudle and Jeschke, 1983; Steudle et al., 1987; Zhu and Steudle, 1991; Figure 4). Figure 4 also shows how root Lp_r has been measured by alternative, steady-state techniques. In the latter techniques, either pressure gradients have been applied (pressure chamber, vacuum), or the osmotic pressure of the medium was varied (for details, see legend to Figure 4 and Zimmermann and Steudle, 1998).

The root pressure probe has been used to separate the axial hydraulic resistance of xylem vessels from that related to flow across the root cylinder (Frensch and Steudle, 1989; Melchior and Steudle, 1993) and to measure the radial hydraulic resistance of individual root zones (Frensch et al., 1996).

Summary of recent results

Some results of root hydraulics are summarized in Table 1. The table separates between herbaceous and woody species. On average, roots from herbs have a root Lp_r which is larger by an order of magnitude than that of woody species. This is due to differences in root structure, namely, to the stronger degree of suberization of woody roots. As for the water, the permeability of woody roots to solutes (permeability coefficients of salts, sugars and the like) is substantially smaller than that of herbs. However, reflection coefficients of woody roots (which denote the 'passive selectivity' of a root) were smaller than those of herbs. In terms of the composite transport model this is understandable. In composite transport systems with parallel arrays, the components (cell-to-cell and apoplastic path) contribute to the overall reflection coefficient according to their hydraulic conductances. Since the permeability of woody roots is lower than that of herbs, the relative contribution of the apoplastic bypass is more significant for the former. In tree roots, differences of up to three orders of magnitude have been found between osmotic and hydraulic water flow (root Lp_r). This remarkable effect has been explained by the model but may, in addition, result from changes in the apoplastic hydraulic conductivity in the presence of pressure gradients (Steudle and Frensch, 1996).

It should be noted that, besides the water, the apoplastic component of transport could be also important for the stress hormone abscisic acid (ABA). When ABA was applied to the root medium, there was a considerable byass flow of ABA in young maize roots, i.e. ABA was transported by solvent drag with the transpiration stream imitated by a vacuum applied to the cut end of the excised roots (Freundl et al., 1998; 1999). In roots of sunflower, the effect was much smaller. The results indicate that the uptake of ABA present in the soil solution in low concentrations, could contribute to the xylem concentration of the hormone. Alternatively and more likely, ABA produced in cells of stressed roots may be delivered to the root apoplast and then transferred to the shoot with the transpiration stream. In both cases, the apoplastic flow of ABA will compensate for the dilution caused by water uptake. Hence, the root-to-shoot signal of ABA may have an apoplastic component which is directly coupled to water uptake, i.e. to transpiration.

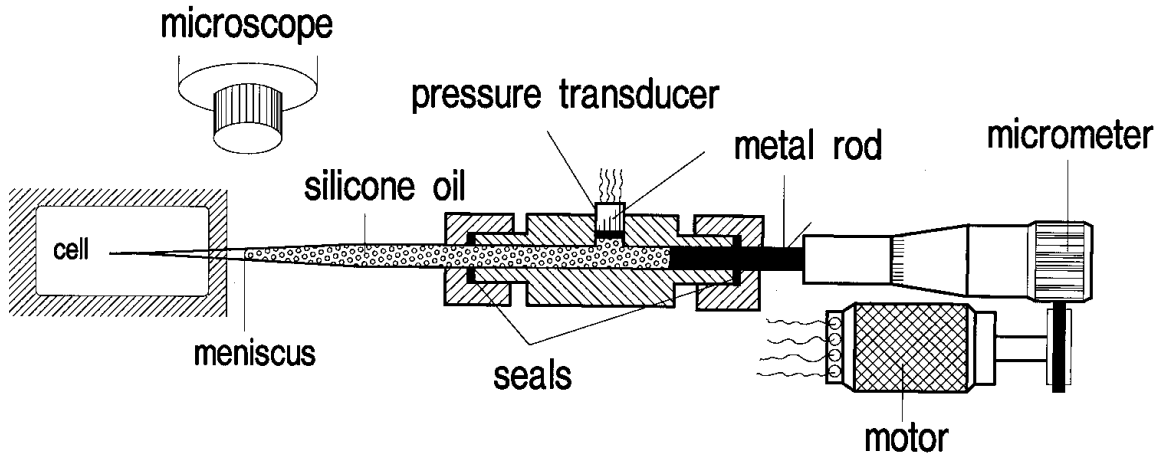

Figure 3. Cell pressure probe for measuring the hydraulic conductivity (water permeability) of plant cell membranes. The tip of the microcapillary is introduced into the cell so that turgor causes a shift of the oil/water meniscus in the tip which can be manipulated by moving the metal rod. Pressure relaxations are produced to work out the hydraulic conductivity of the membrane from half-times of the equilibration of turgor pressure. This requires also the measurement of the elasticity of the cell (also done with the probe) and cell dimensions (cell surface area and volume).

The integration of views

Composite transport provides an integration of views to explain the variability of root water uptake (hydraulic conductivity). Changes in root anatomy and structure have been taken into account such as the formation of apoplastic barriers (Casparian bands) in the endo- and exodermis and of suberin lamellae. The model may be used to integrate effects of water channels (aquaporins) which are much discussed at present. Water channel activity affects the cell-to-cell (protoplastic) rather than the apoplastic component of overall root Lp_r. The model may also account for changes in the driving forces by a dilution of xylem sap ('Fiscus-model'; Steudle and Jeschke, 1983; Steudle et al., 1987). As it stands, it considers parallel transport but serial array of tissues could be incorporated and axial transport in the xylem (Steudle and Peterson, 1998). Special components would be the transport across plasmodesmata (symplastic flow) which has been thought to substantially contribute to overall water flow across roots (Zhang and Tyerman, 1991). In some models, it has been speculated that this component may be affected by pressure gradients across roots (Passioura, 1988). There have been attempts to incorporate the interaction between active solute (nutrient) flow with the water (Steudle, 1989). However, this extension would require detailed knowledge of uptake rates and how this would affect osmotic gradients within and across the root cylinder.

The detailed data obtained so far for root hydraulics (cell and root level) are in agreement with the composite transport model. Pathways are coupled to each other, i.e. water and solutes are exchanged between pathways as they move across. The model explains the differences found between hydraulic and osmotic water flow and the variability of root Lp_r which changes in response to the nature of the driving force and the intensity of flow. Hence, it predicts that root Lp_r may vary according to external conditions (as found). It is proposed that the variability in root Lp_r provides a 'coarse regulation' of water uptake by roots. A 'fine regulation' may be brought about by the action of water channels along the cell-to-cell path. Present work concentrates on the role of water channels during water uptake, i.e., the activity of aquaporins is being mapped in different root tissues. The modes by which water channels are triggered by external and internal signals are currently being worked out (drought, salinity, temperature, nutritional state, heavy metals, etc.). The use of transgenic plants and of plants with reverse genetics play an important role in these studies (see Tyerman et al., 1999, for references). Another important issue is the separation of series hydraulic resistances in the root cylinder, namely, of those of the exodermis and endodermis, and how they would change during root development. Recent data from maize indicate that the development of an exodermis may strongly decrease the overall root Lp_r. The relative contributions of the cell-to-cell and apoplastic

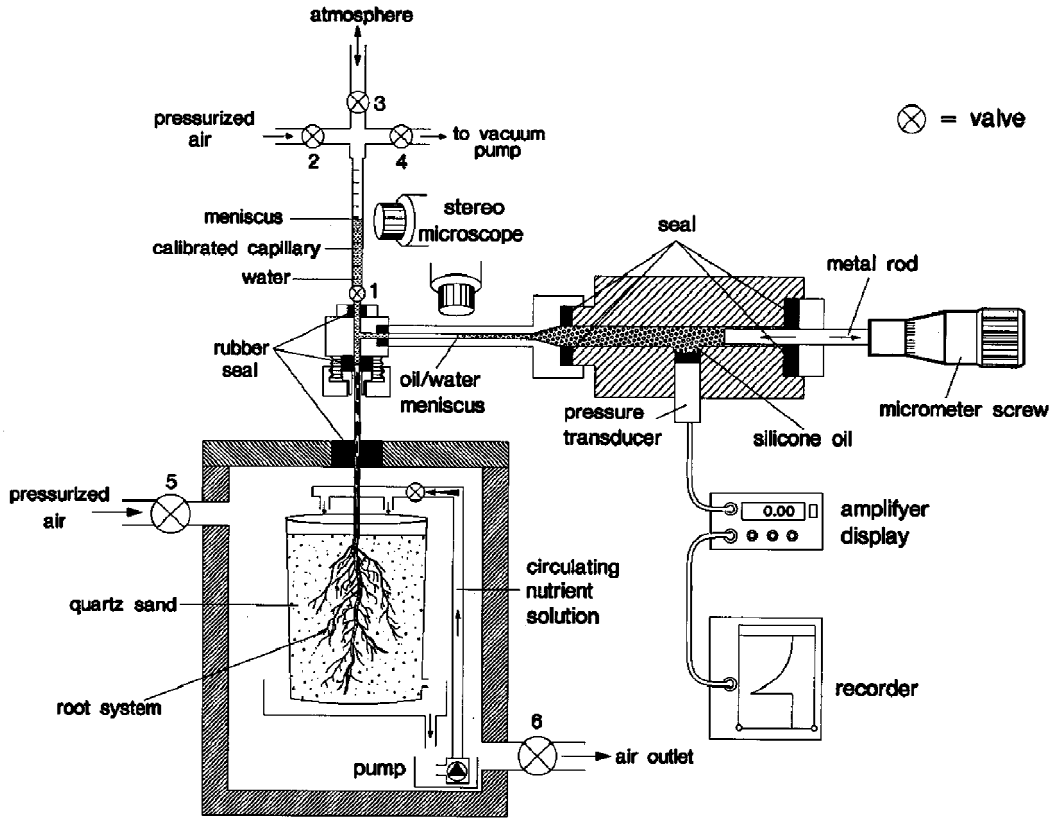

Figure 4. Experimental set-up employed to measure water transport and hydraulic conductivity of excised roots (root systems and individual roots). Different techniques may be used. In one procedure, root exudation is measured while pneumatic pressure is applied to the root system which is tightly sealed in a pressure chamber. The protruding root base is connected to a calibrated capillary. With valves 1 to 5 open and valve 6 closed, the steady water flow across the root (root system) is measured in response to a pneumatic pressure applied to the root. Alternatively, a pressure gradient may be set up by applying vacuum (valve 4 open) or pressurized air (valve 2 open) to the cut root base (xylem; valves 1, 5, 6 open; valve 3 closed). In the absence of pressure gradients (all valves open), water flow may be also measured in response to changes in the osmotic pressure of the root medium. With valve 1 closed and valves 5 and 6 open, the root pressure probe is employed to measure root Lp_r. In this type of experiment, root pressure builds up within the probe which is then changed to induce a water flow, analogous to the procedure used for cells (Figure 3). From the subsequent rate of equilibration of root pressure, root Lp_r is evaluated.

components of radial water flow and how its relative importance would change during root development are further quantified.

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References

Azaizeh H, Gunse B and Steudle E 1992 Effects of NaCl and $CaCl_2$ on water transport across root cells of maize (*Zea mays* L.) seedlings. Plant Physiology 99, 886–894.

Azaizeh H and Steudle E. 1991 Effects of salinity on water transport of excised maize (*Zea mays* L.) roots. Plant Physiology 99, 1136–1145.

Birner T P and Steudle E 1993 Effects of anaerobic conditions on water and solute relations and active transport in root of maize (*Zea mays* L.). Planta 190, 474–483.

Brewig A 1937 Permeabilitätsänderungen der Wurzelgewebe, die vom Spross beeinflusst werden. Zeitschrift für Botanik 31, 481–540.

Brouwer R 1954 The regulating influence of transpiration and suction tension on the water and salt uptake by roots of intact *Vicia faba* plants. Acta Botanica Neerlandica 3, 264–312.

Carvajal M, Cooke D T and Clarkson D T 1996 Responses of wheat plants to nutrition deprivation may involve the regulation of water-channel function. Planta 199: 372–381.

Cheng A C, van Hoek A N, Yeager M, Verkman A S and Mitra A K 1997 Three-dimensional organization of a human water channel. Nature 387, 627–630.

Chrispeels M J and Maurel C 1994 Aquaporins: the molecular basis of facilitated water movement through living plant cells. Plant Physiology 105, 9–15.

Cruz R T, Jordan W R and Drew M C (1992 Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum bicolor* L. following exposure to water deficit. Plant Physiology 99, 203–212.

Fiscus E L 1975 The interaction of osmotic- and pressure-induced water flow in plant roots. Plant Physiology 55: 917–922.

Fiscus E L 1986 Diurnal changes in volume and solute transport coefficients of *Phaseolus* roots. Plant Physiology 80, 752–759.

Frensch J and Steudle E 1989 Axial and radial hydraulic resistance to roots of maize (*Zea mays* L.). Plant Physiology 91, 719–726.

Frensch J, Hsiao T C and Steudle E 1996 Water and solute transport along developing maize roots. Planta 198, 348–355.

Freundl E, Steudle E and Hartung W 1998 Water uptake by roots of maize and sunflower affects the radial transport of abscisic acid and its concentration in the xylem. Planta 207, 8–19.

Freundl E, Steudle E and Harting W (1999) Apoplastic transport of abscisic acid through roots of maize: effects of the exodermis. Planta (*In press*).

Guerrero F D, Jones J T and Mullet J E 1990 Turgor-responsive gene transcription and RNA levels increase rapidly when pea shoots are wilted. Sequence and expression of three inducible genes. Plant Molecular Biology 15, 11–26.

van den Honert T H 1948 Water transport in plants as a catenary process. Discussions of the Faraday Society 3, 146–53.

Henzler T and Steudle E 1995 Reversible closing of water channels in *Chara* internodes provides evidence for a composite transport model of the plasma membrane. J Exper. Bot. 46, 199–209.

Henzler T, Carvajal M, Smyth A, Cooke D T and Clarkson D T 1998 Diurnal variation in root hydraulics and aquaporin gene-homologue expression in *Lotus japonicus*. J. Exper. Bot. 49 S: 10.

Hertel A and Steudle E 1997 The function of water channels in *Chara*: the temperature dependence of water and solute flows provides evidence for composite membrane transport and for a slippage of small organic solutes across water channels. Planta 202, 324–335.

Jap B K and Li H 1995 Structure of the osmoregulated H_2O-channel, AQP-CHIP, in projection at 3.5 Å resolution. J. Molec. Biol. 251, 413–420.

Johansson I, Larsson C, Ek B and Kjellbom P 1996 The major integral proteins of spinach leaf plasma membranes are putative aquaporins and are phoshorylated in response to Ca^{2+} and apoplastic water potential. Plant Cell 8, 1181–1191

Jones H, Tomos A D, Leigh R A and Wyn Jones R G 1983 Water-relation parameters of epidermal and cortical cells in the primary root of *Triticum aestivum* L. Planta 158, 230–6.

Jung J S, Preston G M, Smith B L, Guggino W B and Agre P 1994 Molecular structure of the channel activity of the seed specific aquaporin α-TIP. EMBO Journal 14, 3028–35.

Kramer P J and Boyer J S 1995 Water relations of plants and soils. Academic Press, Orlando.

Maggio A and Joly R J 1995 Effects of mercuric chloride on the hydraulic conductivity of tomato root systems: evidence for a channel-mediated pathway. Plant Physiology 109, 331–335.

Maurel C, Reizer J, Schroeder J L and Chrispeels M J 1993 The vacuolar membrane protein γ-TIP creates water specific channels in *Xenopus* oocytes. EMBO Journal 12, 2241–2247.

Maurel C 1997 Aquaporins and water permeability of plant membranes. Annu. Rev. Plant Physiol. Plant Molec. Biol. 48, 399–429.

Melchior W and Steudle E 1993 Water transport in onion (*Allium cepa* L.) roots. Changes of axial and radial hydraulic conductivities during root development. Plant Physiol. 101, 1305–1315.

Melchior W and Steudle E 1995 Hydrostatic and osmotic hydraulic conductivities and reflection coefficients of onion (*Allium cepa* L.) roots. *In* Structure and Function of Roots. Eds. Baluska F, Ciamporova M, Gasparikova O, Barlow P W. pp 209–213. Kluwer Academic Press Publ., Dordrecht, The Netherlands,

Miller D M 1985 Studies of root function in *Zea mays*. III. Xylem sap composition at maximum root pressure provides evidence of active transport into the xylem and a measurement of the reflection coefficient of the root. Plant Physiol. 77, 162–167.

Murphy R and Smith J A C 1998 Determination of cell water-relation parameters using the presure probe: extended theory and practice of the pressure-clamp technique. Plant Cell Environ. 21, 637–657.

Newman E I 1973 Permeability to water of five herbaceous species. New Phytologist 72, 547–555.

Nielson S and Agre P 1995 The aquaporin family of water channels in kidney. Annual Kidney International 48, 1057–1068.

North G B and Nobel P S 1991 Changes in hydraulic conductivity and anatomy caused by drying and rewetting roots of *Agave desertii* (Agavaceae). Am. J. Bot. 78, 906–915.

Park J H and Saier M H 1996 Phyolgentic characterization of the MIP family of transmembrane channel proteins. J. Membrane Biol. 153, 171–180.

Passioura J B 1988 Water transport in and to roots. Annu. Rev. Plant Physiol. Plant Molec. Biol. 39, 245–56.

Peterson C A and Enstone D E 1996 Functions of passage cells in the endodermis and exodermis of roots. Physiologia Plantarum 97, 592–598.

Peterson C A, Murrmann M and Steudle E 1993 Location of major barriers to water and ion movement in young roots of *Zea mays* L. Planta 190, 127–136.

Peyrano G, Taleisnik E, Quiroga M, de Forchetti S M and Tigier H 1997 Salinity effects on hydraulic conductance, lignin content and peroxidase activity in tomato roots. Plant Physiol. Biochem. 35, 387–393.

Preston G M, Carroll T P, Guggino W B and Agre P 1992 Appearance of water channels in *Xenopus* oocytes expressing red cell CHIP28 protein. Science 256, 385–387.

Reizer J, Reizer A and Saier M H 1993 The MIP family of integral membrane channel proteins: sequence comparisons, evolutionary relationships, reconstructed pathway evolution, and proposed functional differentation of the two repeated halves of the proteins. Critical Reviews in Biochemistry and Molecular Biology 28, 235–257.

Rüdinger M, Hallgren S W, Steudle E and Schulze E D 1994 Hydraulic and osmotic püroperties of spruce roots. J. Exper. Bot. 45, 1413–1425.

Schäffner A R 1998 Aquaporin function, structure and expression: are there more surprises to surface in plant water relations. Planta 204, 131–9.

Schütz K and Tyerman S D 1997 Water channels in *Chara corallina*. J. Exper. Bot. 48, 1511–1518.

Stavosky E and Peterson C A 1993 Effects of drought and subsequent rehydration on the structure, vitality and permeability of *Allium cepa* adventitious roots. Can. J. B. 71, 700–7.

Steudle E 1989 Water flow in plants and its coupling to other processes: an overview. Methods of Enzymology 174: 183–225.

Steudle E 1993 Pressure ropbe techniques: basic principles and application to studies of water and solute relations at the cell, tissue and organ level. *In* Water deficits: plant responses from cell to community. Eds. J A C Smith and H Griffiths. pp 5–36. Bios Scientific Publ. Ltd., Oxford.

Steudle E 1994 Water transport across roots. Plant Soil 167, 79–90.

Steudle E 1995 Trees under tension. Nature 378, 663–4.

Steudle E 1997 Water transport across plant tissue: role of water channels. Biology of the Cell 89, 259–273.

Steudle E and Brinckmann E 1989 The osmometer model of the root: water and solute relations of *Phaseolus coccineus*. Botanica Acta 102, 85–95.

Steudle E and Frensch J 1989 Osmotic responses of maize roots. Water and solute relations. Planta 177, 281–295.

Steudle E and Frensch J 1996 Water transport in plants: role of the apoplast. Plant Soil 187, 67–79.

Steudle E and Henzler T 1995 Water channels in plants: do basic concepts of water transport change? J. Exper. Bot. 46, 1067–1076.

Steudle E and Heydt H 1997 Water transport across tree roots. *In* Trees – Contributions to Modern Tree Physiology. Eds. Rennenberg H, Eschrich W, Ziegler H. pp 239–255. Backhuys Publishers, Leiden, The Netherlands.

Steudle E and Jeschke W D 1983 Water transport in barley roots. Planta 158, 237–248.

Steudle E and Meshcheryakov A B 1996 Hydraulic and osmotic properties of oak roots. J. Exper. Bot. 47, 387–401.

Steudle E, Murrmann M and Peterson C A 1993 Transport of water and solutes across maize roots modified by puncturing the endodermis. Further evidence for the composite transport model of the root. Plant Physiology 103, 335–349.

Steudle E, Oren R and Schulze 1987 Water transport in maize roots. Plant Physiol. 84, 1220–1232.

Steudle E and Peterson C A 1998 How does water get through roots? J. Exper. Bot. 49, 775–788.

Tazawa M, Asai K and Iwasaki N 1996 Characteristics of Hg- and Zn-sensitive water channels in the plasmamembrane of *Chara* cells. Botanica Acta 109, 388–96.

Tyerman, S D, Bohnert H, Maurel C, Steudle E and Smith J A C 1999 Plant water channels: molecular biology meets biophysics. J. Exper. Bot. (*In press*).

Tyree M T 1977 The cohesion-tension theory of sap ascent: current controversies. J. Exper. Bot. 48, 1753–65.

Verkman A S, van Hoek A N, Ma T, Frigeri A and Skach W R 1996 Water transport across mammalian cell membranes. Am. J. Physiol. 270, C12–C30.

Walz T, Typke D, Smith B L, Agre P and Engel A 1995 Projection map of aquaporin-1 determined by electron crystallography. Nature Structural Biology 2, 730–32.

Walz T, Hirai T, Murata K, Heymann J B, Mitsuoka K, Fujiyioshi Y, Smith B L, Agre P and Engel A 1997 The three-dimensional structure of aquaporin-1. Nature 387, 624–627.

Wayne R and Tazawa M 1990 Nature of the water channels in the internodal cells of *Nitellopsis*. J. Membrane Biol. 116, 31–39.

Weatherley P E 1982 Water uptake and flow into roots. *In* Encyclopedia of Plant Physiology Vol 12B. Eds. Lange O L, Nobel P S, Osmond C B, Ziegler H pp 79–109. Springer-Verlag, Berlin.

Zhang W H and Tyerman S D 1991 Effect of low O_2 concentration and azide on hydraulic conductivity and osmotic volume of the cortical cells of wheat roots. Australian J. Plant Physiol. 18, 603–613.

Zhu GL and Steudle E 1991 Water transport across maize roots. Plant Physiol. 95, 305–315.

Zimmermann H M and Steudle E 1998 Apoplastic transport across young maize roots: effect of the exodermis. Planta 206, 7–19.

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