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# Water uptake by roots: effects of water deficit

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## Abstract

**The variable hydraulic conductivity of roots ($Lp_r$) is explained in terms of a composite transport model. It is shown how the complex, composite anatomical structure of roots results in a composite transport of both water and solutes. In the model, the parallel apoplastic and cell-to-cell (symplastic and transcellular) pathways play an important role as well as the different tissues and structures arranged in series within the root cylinder (epidermis, exodermis, cortex, endodermis, stelar parenchyma). The roles of Casparian bands and suberin lamellae in the root's endo- and exodermis are discussed. Depending on the developmental state of these apoplastic barriers, the overall hydraulic resistance of roots is either more evenly distributed across the root cylinder (young unstressed roots) or is concentrated in certain layers (exo- and endodermis in older stressed roots). The reason for the variability of root $Lp_r$, is that hydraulic forces cause a dominating apoplastic flow of water around protoplasts, even in the endodermis and exodermis. In the absence of transpiration, water flow is osmotic in nature which causes a high resistance as water passes across many membranes on its passage across the root cylinder. The model allows for a high capability of roots to take up water in the presence of high rates of transpiration (high demands for water from the shoot). By contrast, the hydraulic conductance is low, when transpiration is switched off. Overall, this results in a non-linear relationship between water flow and forces (gradients of hydrostatic and osmotic pressure) which is otherwise hard to explain. The model allows for special root characteristics such as a high hydraulic conductivity (water permeability) in the presence of a low permeability of nutrient ions once taken up into the stele by active processes. Low root reflection coefficients are in line with the idea of some apoplastic bypasses for water within the root cylinder. According to the composite transport model, the switch from the hydraulic to the osmotic mode is purely physical. In the presence of heavily suberized roots, the apoplastic component of water flow may be too small. Under these conditions, a regulation of radial water flow by water channels dominates. Since water channels are under metabolic control, this component represents an 'active' element of regulation. Composite transport allows for an optimization of the water balance of the shoot in addition to the well-known phenomena involved in the regulation of water flow (gas exchange) across stomata. The model is employed to explain the responses of plants to water deficit and other stresses. During water deficit, the cohesion–tension mechanism of the ascent of sap in the xylem plays an important role. Results are summarized which prove the validity of the coehesion/tension theory. Effects of the stress hormone abscisic acid (ABA) are presented. They show that there is an apoplastic component of the flow of ABA in the root which contributes to the ABA signal in the xylem. On the other hand, (+)-*cis-trans*-ABA specifically affects both the cell level (water channel activity) and water flow driven by gradients in osmotic pressure at the root level which is in agreement with the composite transport model. Hydraulic water flow in the presence of gradients in hydrostatic pressure remains unchanged. The results agree with the composite transport model and resemble earlier findings of high salinity obtained for the cell ($Lp$) and root ($Lp_r$) level. They are in line with known effects of nutrient deprivation on root $Lp_r$ and the diurnal rhythm of root $Lp_r$ recently found in roots of *Lotus*.**

Key words: Composite transport, hydraulic conductivity, regulation, root, stress, water deficit, water uptake.

## Introduction

Many efforts have been made in the past to understand the water balance of plants in terms of a regulation of

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transpiration, i.e. of how stomatal conductance would be affected by water status, light intensity, nutrition, and other factors and how this would change under stress conditions such as during deficits in water supply (Cowan, 1977; Schulze, 1986; Kramer and Boyer, 1995; Jones, 1998). Fewer efforts have been made to investigate the input side of the water balance, i.e. the acquisition of water from the soil. It has been known for a long time that the hydraulic conductance of roots is variable (Brewig, 1937; Brouwer, 1954; Weatherley, 1982; Steudle *et al.*, 1987; Steudle, 1994; Steudle and Peterson, 1998; Henzler *et al.*, 1999). It depends on factors such as water shortage and salinity of the soil and on the demands for water from the transpiring shoot. Other important factors are nutrient deficiency, anoxia, temperature, and heavy metals (Munns and Passioura, 1984; Radin and Eidenbock, 1984; Azaizeh *et al.*, 1992; Birner and Steudle, 1993; Maggio and Joly, 1995; Carvajal *et al.*, 1996; Peyrano *et al.*, 1997; Schreiber *et al.*, 1999; Henzler *et al.*, 1999; Clarkson *et al.*, 2000). The lack in current knowledge of how these factors influence water supply is largely due to technical problems in measuring, in sufficient detail, the hydraulic architecture of roots. Basic hydraulic properties of roots are not yet adequately understoood, simply because roots in the soil are much less accessible than shoots. Comparative measurements of root hydraulics (different species, treatments etc.) require measurement of water flows, driving forces (pressure and osmotic gradients between root surface and xylem) and root surface area. Since growing conditions change the root structure and anatomy, this has to be characterized as well.

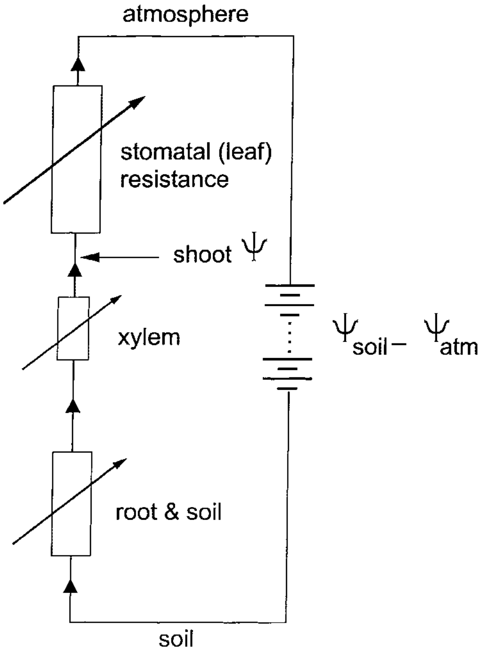


**Fig. 1.** Simplified model of steady water flow across a plant. Water uptake by roots, long-distance transport in the xylem and the stomatal resistance are denoted by variable hydraulic resistors arranged in series. Usually, the resistance of the root is smaller than that of the shoot which is dominated by resistances of vapour pathways in the leaf and the boundary layer outside the leaf. The resistance along the xylem is relatively small. Hence, at a given water flow through the system, the root hydraulic resistance in relation to that of stomata will determine the water status (water potential) of the shoot (arrow). In order to improve the water status of the shoot ($\psi_{shoot}$), the plant can either improve water uptake by reducing $R_{root}$ or avoid water losses by increasing $R_{shoot}$.

In a schematic way, it is shown in Fig. 1 how the variable root hydraulic resistance would contribute to the water potential (water status) of the shoot. Usually, the vapour pathways in mesophyll air spaces, stomatal pores, and the boundary layer outside the leaves represent the highest hydraulic resistance in the soil–plant–air continuum (SPAC), and most of the water potential difference between soil and atmosphere will drop here (Nobel, 1991; Yang and Tyree, 1994). At a given water potential difference ($\psi_{soil}$–$\psi_{atm}$) and water flow across the soil–plant–air continuum, the water potential of the shoot may be dominated by the drop in water potential across the root hydraulic resistance which is usually the highest within the liquid part of the SPAC. In other words, to improve the water status of the shoot, the plant could either increase stomatal or decrease root hydraulic resistance; the latter does happen (besides the regulation of transpiration). It is not clear whether or not this is a purely physical adjustment or involves some active regulation of root hydraulic properties (besides the stress-induced changes in anatomy which are obvious). As indicated in the figure, the hydraulic resistance of the xylem is relatively small. It may, however, become important under conditions of stress, when high tensions in the xylem cause cavitation and interrupt water flow in vessels between root and shoot (Tyree and Sperry, 1988).

It is generally accepted that the contribution of active water transport in plants, i.e. water flow *directly* coupled to metabolic reaction(s), should be negligible. This is because the water permeability of plant cell membranes is larger by several orders of magnitude than that of solutes which would cause a rapid short circuit of primary active water flow (Steudle, 1989, 1992). Instead of actively taking up water, roots just allow it to pass through them in response to water potential gradients usually set up by transpiration. The complex anatomical structure of roots results in a complex pattern of water flow. Transport across various tissues (epidermis, cortex, stele) has to be considered during the radial passage across the root cylinder as well as a longitudinal flow component (axial transport in xylem vessels). During stress, the anatomy of root tissue will change, largely, because stress (such as water deficit) induces the development of apoplastic barriers for water and ion flow (Stasovski and Peterson, 1991; Taleisnik *et al.*, 1999). Their formation represents a fundamental adaptive strategy of plants to survive in an adverse environment (North and Nobel, 1995; Peyrano *et al.*, 1997; Zimmermann and Steudle, 1998; Schreiber *et al.*, 1999; Zimmermann *et al.*, 2000). In addition, the hydraulic conductivity of root cell membranes may be reduced due to a closure of water channels or aquaporins in root cell membranes. These transport proteins have received much attention in the past years (Chrispeels and Maurel, 1994; Steudle and Henzler, 1995; Maurel, 1997; Steudle and Peterson, 1998; Tyerman *et al.*, 1999; Kjellbom *et al.*, 1999). So, besides transport across the apoplast, there is some water flow across cell membranes. Different from the irreversible chemical modifications of the apoplast (Casparian bands, suberin lamellae), the intensity of the cellular component may be either reversibly regulated by an opening or closing of existing water channels or the density or aquaporins may be increased by recruitment of internalized protein into the plasma membrane. During root development the relative contribution of components of overall water flow may change, when the endodermis and exodermis develop (Frensch *et al.*, 1996). Water deficits reduce root growth and cause a pronounced suberization of the apoplast and, perhaps, also affect the cellular passage (water channels). This influences the water balance by reducing the capacity of roots to take up water.

The radial flow of water across plant roots along the apoplast with its barriers and the parallel cell-to-cell path (aquaporins) is best described by a composite transport model which allows for differences in movement through individual cell layers such as the exo- and endodermis, as well as through various tissues (Steudle *et al.*, 1993, 1999; Steudle, 1994, 1997; Steudle and Frensch, 1996; Steudle and Peterson, 1998). The model allows for an interaction between parallel flows. The axial component of water flow may be incorporated (Frensch and Steudle, 1989; Steudle and Peterson, 1998).

In this review, some basic properties of root water transport and how they would change during conditions of water deficit are discussed. The focus will be on the relative roles of apoplastic barriers and aquaporins, but changes in the driving forces according to the cohesion–tension mechanism of the ascent of sap will also be considered. Some recent results of the effects of the stress hormone abscisic acid (ABA) will be included and measurements in which changes in the chemical composition of apoplastic barriers have been correlated with measurements of the hydraulic properties of roots both at the cell and whole root levels (Freundl *et al.*, 1998, 2000; Hose *et al.*, 2000; Zimmermann and Steudle, 1998; Zimmermann *et al.*, 2000). This review will also refer to older data on the effects of salinity and more recent work on nutrient stresses and diurnal aquaporin expression which may be important with respect to water deficit (Azaizeh and Steudle, 1991; Azaizeh *et al.*, 1992; Henzler *et al.*, 1999; Clarkson *et al.*, 2000).

## Role of root anatomy: the apoplast

The interpretation of root hydraulic data requires sufficient knowledge of their structure. Namely, this refers to the development of suberin lamellae and Casparian bands in the apoplast. There are major differences among species and growing conditions. In the past few years there has been important progress in characterizing apoplastic barriers caused by drought and other environmental factors. In maize, the absorption of water and nutrient ions may be significantly reduced during drought stress (Stasovsky and Peterson, 1991). Stressed roots developed a suberized interface between living tissue and rhizosphere to minimize water losses. It appeared that, upon rehydration, root systems recovered their hydraulic conductance (which, however, was not measured) by elongation growth thus forming new roots of high hydraulic conductivity. Taleisnik *et al.* grew plants under conditions of water shortage and controls and compared the ability of roots to retain water from plants which have an exodermis with those which do not (Taleisnik *et al.*, 1999). Rates of water loss were smaller in exodermal than in non-exodermal roots. Older parts of roots released less water to the dry environment than younger. Rieger and Litvin concluded from hydraulic measurements on root systems (drought-stressed and controls) of intact plants of different herbaceous and woody species that the existence of a suberized exodermis had some influence on the overall root $Lp_r$ (Rieger and Litvin, 1999). However, the resistance of the cortex appeared to be of equal or even greater importance than that of the suberized layers. Recent measurements on excised roots of young maize seedlings have shown that the hydraulic conductivity was larger by a factor of 3.6 (on average) when there was no exodermis (roots grown in hydroponic culture) as compared with roots having an exodermis (roots grown in aeroponics) (Zimmermann and Steudle, 1998). In these experiments, a possible effect of a change of the hydraulic conductivity of root cell membranes (water channels) has been excluded by measuring the root cell $Lp$ (cell pressure probe) besides the overall root $Lp_r$ (root pressure probe; Zimmermann *et al.*, 2000). Hence, there was a substantial effect of suberization on the overall hydraulic properties of roots.

In the past few years there has been considerable progress in identifying the chemical composition of apoplastic barriers. After digesting away the rest of the root, it has been possible to separate Casparian bands from the exo- and endodermis and to analyse these structures chemically and to refer the results to root hydraulic properties (Schreiber, 1996; Zeier and Schreiber, 1998; Schreiber *et al.*, 1999; Zimmermann *et al.*, 2000). The results show that Casparian bands contain both aliphatic and aromatic suberin. The former is thought to be more hydrophobic and less permeable to water, the latter is a lignin-like phenolic polymer esterified with hydroxycinnamic acids. In addition, Casparian bands contain considerable amounts of lignin. Since lignin is a relatively hydrophilic compound, the analyses from Schreiber's group suggest that Casparian bands would be fairly impermeable to ions and to rather big polar solutes, but may allow some passage of water and small solutes. This is in agreement with transport measurements.

## Nature of water movement in roots

In textbooks, the movement of water in roots is often described as an osmotic process in which root membranes play the important role (Kramer and Boyer, 1995). The root is looked at as a nearly perfect osmometer. Hydraulic resistances involved in the radial movement of water are thought to be constant. However, evidence collected during the past decade indicates that this view has to be modified. Along the apoplastic path, water movement will be hydraulic in nature, i.e. driven by gradients in hydrostatic pressure. Different from cell membranes, cell walls have no selective properties, i.e. they do not select between water and solutes as they pass through. Hence, gradients in solute concentration or osmotic pressure along the apoplast ($\Delta\pi_s$, where the subscript 's' stands for solute) do not result in a significant water flow. This is so because, in the apoplast, the osmotic component of water potential has to be modified by a reflection coefficient ($\sigma_s^{cw}$, where the additional superscript 'cw' stands for 'cell wall'), which is a measure of the 'passive selectivity' of the apoplast. The reflection coefficient of the apoplast will usually be close to zero, so that the 'effective' osmotic component of water potential which drives the flow across the apoplast, i.e. $\sigma_s^{cw}\Delta\pi_s$, will be also small. Along the cell-to-cell path, the situation is different because of the presence of membranes which exhibit a $\sigma_s \approx 1$. The overall root $\sigma_{sr}$ will be between zero and unity as found in experiments with the root pressure probe and other techniques (Miller, 1985; Steudle *et al.*, 1987, 1993; Steudle and Frensch, 1989; Steudle and Peterson, 1998). As a consequence of their composite structure, roots do not behave like ideal osmometers which would exhibit a reflection coefficient of unity. In addition to the low reflection coefficient of roots, the hydraulic conductivity of roots should depend on the force (osmotic and hydrostatic pressure gradients) used to drive water across roots. This is also a consequence of composite transport. In the presence of different forces, the two pathways (apoplastic and cell-to-cell) will be used with different intensity. Both pathways will be used in the presence of a hydraulic (hydrostatic pressure) gradient such as during transpiration. In the presence of an osmotic gradient, however, cell-to-cell transport will dominate. The hydraulic component will be small if any. As a consequence, the hydraulic conductivity of roots should differ depending on the conditions as found experimentally (see below).

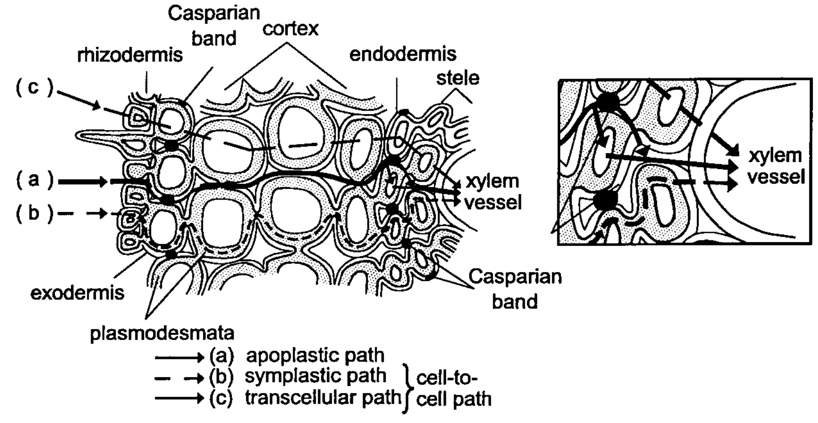
## Pathways for water and solutes and composite transport

When water and solutes (nutrients) move into a root, there will be a cellular (cell-to-cell) and an apoplastic component of flow (Steudle, 1989, 1992). The passive cell-to-cell component of solute flow should be small because of the low permeability of solutes to membranes (nutrient ions). For water this is different, because water moves by several orders of magnitude more rapidly across membranes than do ions. In principle, the cell-to-cell ('protoplastic') component would have to be split into a symplastic and a transcellular component (Fig. 2A). The former is the component due to transport across plasmodesmata within the symplast. The latter refers to the passage across plasmalemmata (two membranes per cell layer). The vacuolar component is not included, the contribution of which should be small (Steudle and Peterson, 1998). Experimentally, the symplastic and transcellular components can not be separated to date. Therefore, they are summarized for pragmatic reasons as a cell-to-cell component. During the radial passage of water across the root, there could be combinations of pathways in that water may travel within the symplast for some distance and may then cross the plasma membrane and move within the cell wall. These combinations can be included in models for water transport as long as allowance is made for a rapid exchange of water between pathways ('local equilibrium'; Molz and Ferrier, 1982; Westgate and Steudle, 1985; Steudle, 1989, 1992; Steudle and Frensch, 1996). According to these models, the contribution of the cell-to-cell component can be derived from measurements with the cell pressure probe. The apoplastic component (which is, to date, not accessible to direct measurement in intact tissue) is obtained from the difference between the hydraulic conductivity of the whole root and that of the cell-to-cell component (Zhu and Steudle, 1991). When apoplastic barriers are formed which interrupt the flow around root protoplasts in the endo- and exodermis along a developing root, the relative contributions of hydraulic and osmotic flow change (Frensch *et al.*, 1996).

The composite structure of roots allows a fairly high and adjustable water permeability in the presence of a pronounced ability to retain nutrient salts transferred into the xylem (low solute permeability). This would be hard to achieve with a homogeneous membrane or osmotic barrier. The composite transport model explains experimental findings such as (i) low root reflection coefficients, (ii) differences between osmotic and hydraulic water flow and the variability of root $Lp_r$, and (iii) differences between roots of woody and herbaceous plants.

Low reflection coefficients can be simply explained by the existence of apoplastic bypasses in arrays where Casparian bands have not yet developed or even by some

A: Transport pathways in roots



B: Composite transport model of root

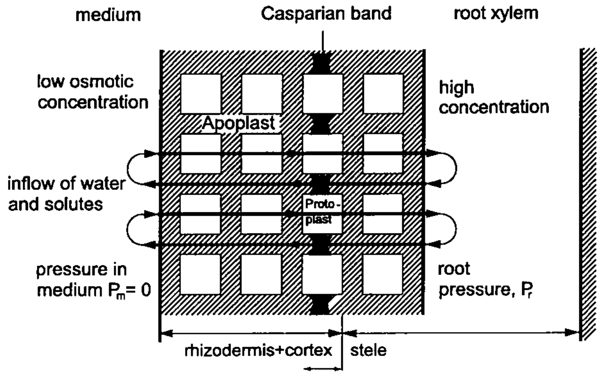


**Fig. 2.** (A) Routes of radial flow of water across plant roots. The apoplastic path is around protoplasts. The symplastic path is mediated by plasmodesmata which bridge the cell walls between adjacent cells so that a cytoplasmic continuum is formed. During the passage along the apoplast and symplast, no membranes have to be crossed. On the transcellular path, two plasma membranes have to be crossed per cell layer. The transcellular path is something special for water which has a high membrane permeability (cell hydraulic conductivity). Usually, this component is negligible for solutes. Note that the symplastic and transcellular flow components can not be separated experimentally and are summarized as a cell-to-cell component of water flow (see text). Due to the rapid water exchange between protoplasts and adjacent apoplast, there should be local water flow equilibrium between the two compartments at any time. In the endodermis and exodermis of roots, the apoplastic flow component can be modified by the existence of apoplastic barriers (Casparian bands, suberin lamellae). These are usually thought to be impermeable for water and solutes (nutrient ions). (B) The complex composite structure of roots causes 'composite transport'. This is due to the fact that along the apoplastic path there are no membranes and, hence, there is no osmotic water flow because of a wall reflection coefficient of nearly zero. On the other hand, there is a considerable hydraulic flow across the apoplast. Across the cell-to-cell path, both flow components (hydraulic and osmotic flow) are present, but this passage has a relatively high hydraulic resistance because there are a lot of membranes which have to be crossed. There will be no hydraulic water flow across the apoplast in the absence of hydrostatic pressure gradients (at zero transpiration). Osmotic flow will be small, because of the high resistance under these conditions. Depending on the efficiency of apoplastic barriers, this results in large differences between hydraulic and osmotic flow which causes variability of root $Lp_r$. Tensions in the xylem play an important role. At zero or low water flows, a circulation flow of water can be set up within the root as indicated. Note that, different from (A), only one Casparian band is shown in (B) for the sake of simplicity. The atmospheric pressure of the root medium is taken as a reference of pressure, i.e. $P_m = 0$.

bypass flow of water across the Casparian band itself (Fig. 2B). They are supported by combined measurements of cell *Lp* and root $Lp_r$ and by puncturing experiments (Zhu and Steudle, 1991; Azaizeh *et al.*, 1992; Steudle *et al.*, 1993; Peterson and Steudle, 1993). The existence of parallel elements of low (apoplast) and high (cell-to-cell) reflection coefficients should result in a circulation flow of water in the root at zero overall water flow (Fig. 2B), which can be demonstrated in computer simulations in which overall flows (water, solutes) and reflection coefficients have been calculated using measured root cell data (W Melchior and E Steudle, unpublished results). Differences between hydraulic and osmotic water flow are considerable and more pronounced in roots of woody than herbaceous plants. In woody species, they can be as large as two to three orders of magnitude (Rüdinger *et al.*, 1994; Steudle and Meshcheryakov, 1996; Steudle and Heydt, 1997). This is in line with the theory. The variable root $Lp_r$, is largely explained by a change in the driving force (see below), but other reasons have been discussed as well (Fiscus, 1975; Passioura, 1988).

## Physiological consequences of composite transport

The most obvious consequence of composite transport is that water supply of the shoot by the root may change according to the demand of the shoot, simply by a 'physical adjustment' of root $Lp_r$. In a transpiring plant, the hydrostatic pressure gradient between soil solution and xylem will be high (tensions in the xylem), and the hydraulic resistance of the root low. This facilitates water uptake with increasing demand. It appears that there is a 'switching' between the hydraulic and osmotic modes of action of roots. On the other hand, the hydraulic resistance will be high at low rates of transpiration, i.e. during the night or during periods of water deficit. Under these conditions, plants may be protected from excessive water loss to the soil by the high hydraulic resistance of its roots. Thus, the model tends to optimize the water balance by adjusting root hydraulics according to the demand from the shoot (Fig. 1). The leak rate for solutes (nutrient salts) is kept low throughout. Typically, permeability coefficients of roots to nutrient salts are similar to those of cell membranes (Steudle and Brinckmann, 1989).

## Role of the endodermis and exodermis

Measurements with excised roots of young maize seedlings grown in hydroponic culture have shown that the hydraulic resistance is not concentrated in the endodermis (which would be the conventional view). When grown in hydroponics, roots developed no exodermis (Peterson and Steudle, 1993; Peterson *et al.*, 1993; Steudle *et al.*, 1993). Rather than being concentrated in the endodermis, the resistance was more evenly distributed in the living root tissue. Vessel walls which were already thickend and contained lignin, contributed to only 10–30% of the overall resistance to water movement. The endodermis was modified by Casparian bands, but there were no suberin lamellae. So, the conclusion that the endodermis (with Casparian bands only) was not a major barrier to water movement could only be drawn for these young roots grown in hydroponics. In roots grown under 'real' conditions, extrapolation from the measurements on roots grown in aeroponics and from other results indicated that this is not usually the case. Definitely, the exodermis represents a barrier for water movement for maize roots grown under real conditions. It is expected that suberin lamellae laid down in the tangential, radial and transverse walls reduce the hydraulic conductivity. The same may occur after the thickening of both layers which may be suberized and/or lignified. There are experiments which show that this is true (North and Nobel, 1991, 1995; Melchior and Steudle, 1993).

During water stress, the formation of suberin lamellae in the endo- and exodermis could result in localized high resistances for water and ion flow in the root apoplast. The exodermis could, thus, contribute to the regulation of water uptake into roots as suggested by experiments in which roots were grown in soil with water deficits or nutrient solution with high salinity (Stasovski and Peterson, 1991; Cruz *et al.*, 1992; Azaizeh and Steudle, 1991; Azaizeh *et al.*, 1992; Peyrano *et al.*, 1997; Taleisnik *et al.*, 1999). However, recent measurements on young onion roots grown in vermiculite have shown that root $Lp_r$ increased as the exodermis developed at constant cell $Lp$ (Barrowclough *et al.*, 2000). These results indicate that, different from maize, the hydraulic resistance may be more evenly distributed across the root cylinder in onion even during stages where the exodermis is already developed. To date, there are, for technical reasons, no quantitative values of the permeability of the exo- and endodermis of intact roots to water. These detailed measurements are necessary to work out the functions of the two structures during water deficit and other conditions of stress. Although limited in application, the approach of Zimmermann and Steudle already mentioned may be used in which a variation of growing conditions produced roots with or without an exodermis (Zimmermann and Steudle, 1998). Another approach would imply measurements of changes in cell $Lp$ and of the propagation of changes in water potential (osmotic and hydrostatic pressure) across the root cylinder (cell pressure probe). These experiments are not easy to perform, but the techniques for making them are, in principle, developed (Zhu and Steudle, 1991). They should be used to see how hydraulic resistances of the two layers would change in response to water deficits. Suberized cells of the exo- and endodermis should have a smaller cell $Lp$. Hence, rates of the propagation of changes in water potential of the root medium across the root (as measured with the cell pressure probe in cortex cells) should be smaller in the presence of a suberized exodermis.

## Solute transport

Water is much more mobile along both the apoplastic and cell-to-cell path than solutes. Therefore, the movement of water in the apoplast can not be quantified by following the movement of apoplastic dyes. For example, in the experiments of Zimmermann and Steudle, the external media contained the ionic apoplastic tracer PTS (3-hydroxy-5,8,10-pyrene-trisulphonate; Peterson *et al.*, 1981; Hanson *et al.*, 1985; Skinner and Radin, 1994) to test the permeability of the roots of this ionic compound besides the water (Zimmermann and Steudle, 1998). PTS passed across the roots and, different from the water, the permeability of PTS was the same regardless of whether or not the root had a mature exodermis. During its passage across the root, PTS was diluted to a concentration as low as 0.2% of that in the medium. If PTS were a good tracer for water, this would mean that the apoplastic component of water flow was only 0.2%. This, however, was not true, because the comparison between root $Lp_r$ and root cell $Lp$ showed that there must have been a considerable flow of water around protoplasts. This is also indicated from measurements on species other than maize (Radin and Matthews, 1989). It was concluded that, at least for roots of maize plants grown in aeroponics up to an age of 3 weeks, the endodermis rather than the exodermis was the main barrier for the PTS flow so that the development of the exodermis did not result in a measurable decrease of the PTS flow. It appears that charged solutes are effctively retained in the presence of Casparian bands.

The picture of the root depicted so far is that of a structure in which the apoplast still has some permeability to water, even in the exo- and endodermis. This conclusion was drawn from both the comparison between root $Lp_r$ and cell $Lp$ and from the chemical analysis of apoplastic barriers (see above). It does not refer to nutrient ions. In young maize roots, there was a rapid decrease in root pressure, even when only a few cells of the endodermis were injured (Steudle *et al.*, 1993). As for PTS, the diffusion of ions out of the stele was strongly impeded by the endodermis. The rapid decline of root pressure following an injury suggested that there was a bulk flow of xylem solution across the leak which constituted a low-resistance pathway between a compartment of higher pressure (stelar apoplast) and one of lower pressure (medium). The results confirmed that the endodermis acts as an efficient barrier to the back-diffusion of ions released into the apoplast of the stele, which allows root pressure to build up under conditions of low transpiration. On the other hand, the hydraulic resistance of the endodermis is rather low, at least for cells with just Casparian bands. Thus, the transport properties of roots are optimized for both ions and water. The former are taken up selectively and are held safely in the stele, while the resistance to water flow is low, allowing a sufficient supply to the shoot.

## Are water channels the alternative passage?

In the shoot, water flow is largely controlled by stomates. Stomata represent an 'active' element of control or regulation which is tuned by the water status of the shoot and signals from the root (ABA). The cuticle of the shoot can be regarded as 'water-tight' or nearly so. In the root, the situation is less clear. There are no stomates and water and nutrient uptake require a passage across arrays of non-suberized tissue. On the other hand, the hydraulic conductivity has to be reduced to avoid substantial water losses to the dry soil when transpiration is switched off. It appears that, to some extent, the composite transport model solves the dilemma. According to the model, there is a variable root resistance which is low in the presence of transpiration, when the tension (negative pressure) in the xylem provides a water potential gradient which is sufficient to take up water even from a dry soil. In the absence of transpiration (e.g. at night), suberization of roots (at water deficits) provides a minimization of water losses to the dry soil, when the water potential gradient is in the wrong direction. It should be noted that matric forces are equivalent to hydrostatic forces (as are osmotic forces), but they are physically different. This may cause differences in their role as a driving force. Matric forces originate from the component of water potential which derives from surface tension effects rather than from volume work which is the origin of the hydrostatic pressure component. With respect to the model, it is important how changes in the matric potential of the soil are translated into changes of components of water potential in the root apoplast (as shown in detail by Steudle, 1992). When changes cause a change in the osmotic component, the resulting flow would be largely from cell to cell (high resistance). On the other hand, when they cause a gradient in hydrostatic pressure or matric potentials, the flow will be largely apoplastic (low resistance). At a substantial water shortage in the soil, the hydraulic resistance of the root may be too high to allow for a sufficient acquisition of water, even when water potential gradients are in the right direction. Under these conditions, water channels may act as valves to reversibly increase the hydraulic conductivity and allow for a water uptake under adverse conditions. It has been shown that water channels can be activated by phosphorylation which, in turn, is affected by factors such as water potential, turgor, or $Ca^{2+}$ concentration in the apoplast (Johansson *et al.*, 1996; Kjellbom *et al.*, 1999). To date, current understanding of how this regulation takes place in the intact root is fairly limited.

For roots of *Lotus japonicus* it has been demonstrated that the concentration of the mRNA encoding for putative water channels displayed a distinct diurnal rhythm with a maximum at noon. This coincided with the maximum in the root hydraulic conductivity measured with either osmotic or pressure gradients. However, maxima in root $Lp_r$ were not correlated with appropriate changes in the hydraulic conductivity of root cortex cells as shown by measurements with the cell pressure probe. The result was interpreted in that regulation of cell $Lp$ may be confined to endodermal and stelar cells only as suggested by molecular markers (Schäffner, 1998). In the stele, a regulation would be more efficient, anyhow, because, for geometric reasons, this part contributes more to overall radial resistance than the cortex and epidermis.

For some species such as bean (*Phaseolus coccineus*) and barley, it has been demonstrated that, due to a high membrane *Lp*, the cell-to-cell passage dominates (Steudle and Jeschke, 1983; Steudle and Brinckmann, 1989). For others, the effects are variable. A few attempts have been made to demonstrate the action of water channels (aquaporins) in roots such as by closing them with mercurials (Maggio and Joly, 1995). However, in these experiments effects of the blocking agent on other transporters and side effects have not been completely ruled out. Experiments on wheat indicated that nutrient deprivation reduced water channel activity (Carvajal *et al.*, 1996; Clarkson *et al.*, 2000). The conclusion was drawn from the fact that, different from controls, the hydraulic conductivity of deprived roots was not affected by mercurials. Recently, Zhang and Tyerman have used the cell pressure probe to measure the reversible inhibition of water channels by $HgCl_2$ in cortical cells of wheat roots (Zhang and Tyerman, 1999). Interestingly, hypoxia caused similar effects as $HgCl_2$ and hypoxia-treated cells could not be further inhibited. Zhang and Tyerman did not measure the effect of closure of water channels on root $Lp_r$ as did other authors (Azaizeh and Steudle, 1991; Azaizeh *et al.*, 1992). The latter authors found that, in maize, salinity (100 mM) caused a reduction of cell *Lp* by factor of three to six. However, at the root level, the reduction was only 30–60%. The result has been explained in terms of the composite transport model by a substantial apoplastic bypass-flow of water.

For intact internodes of *Chara*, there are, to date, detailed data on the function of water channels (Henzler and Steudle, 1995; Schütz and Tyerman, 1997; Hertel and Steudle, 1997). The work demonstrated both the selectivity of water channels and its significance for cell *Lp*. Similar to the wheat cortex cells (Zhang and Tyerman, 1999), closure of water channels reduced cell *Lp* by 75%. On the other hand, the permeability of the membrane for small uncharged solutes such as low molecular weight alcohols, amides, ketones etc., did not change. A careful inspection of the transport properties of these cells indicated that there was some slippage of the solutes across the water channels (Steudle and Henzler, 1995; Hertel and Steudle, 1997; Heuzler and Steudle, 2000). According to the results with *Chara*, water channels in plants do not appear to be as selective as has been sometimes proposed (Chrispeels and Maurel, 1994; Maurel, 1997; Schäffner, 1998). There is a lack of combined measurements at both the root and cell level to evaluate the effects of channel blockage on overall transport. These measurements have to include cells of the exo- and endodermis and stelar cells.

## The cohesion–tension mechanism provides the switching between different modes of transport in roots

The non-linear force/flow relationship found during water uptake by plant roots is favourable for the plant. It allows the intensification of water flow during periods of a high demand from the transpiring shoot. At water shortage, however, the hydraulic resistance would be high, thus preventing a backflow to the dry soil when transpiration is switched off. The phenomenon of a variable root resistance has been interpreted in different ways. It has been interpreted in terms of changes in the water permeability of root cell membranes (Brewig, 1937). Fiscus developed a physical model which explained the 'apparent' decrease of root hydraulic resistances at high flow rates by a change in the driving force (Fiscus, 1975). According to the 'dilution model' of Fiscus, the change was due to a change in the osmotic component of the driving force at a constant root $Lp_r$. Under conditions of water shortage, the effect should increase as the significance of the osmotic pressure of the xylem sap increases. However, detailed measurements with pressure probes have shown that the dilution effect can not completely explain non-linearity (Zimmermann and Steudle, 1998).

Tensions in the root xylem provide the major force moving water across the root cylinder into xylem vessels and up to the shoot. Only occasionally, should osmotic forces dominate. Hence, the cohesion–tension mechanism plays an important role during the acquisition of water by roots, namely, under conditions of water stress. During the past ten years, the validity of the cohesion–tension theory has been questioned by Zimmermann and co-workers on the basis of direct measurements of xylem pressure using the cell pressure probe (Balling and Zimmermann, 1990; Melcher *et al*, 1998). In the early papers from this group, tensions in the xylem were rather low (pressures less negative), and were hardly affected by transpiration. Very often sub-atmospheric pressures have been measured rather than pressures below the absolute zero (vacuum). Values of $P_x$ as measured with the pressure probe were substantially higher (less negative) than those found with the Scholander bomb (pressure chamber). Zimmermann and co-workers concluded that the cohesion theory was wrong and that the pressure chamber did not correctly measure water potentials (xylem pressure, $P_x$). However, as the group improved its skills in measuring xylem pressure, values became more negative and tensions of up to 0.5–0.6 MPa were found which reacted on transpiration. It was now concluded that the cohesion–tension mechanism can not be completely excluded. Rather, it would serve as an additional mechanism. The change in the attitude may indicate that, after all, the group is on its way to accept the cohesion–tension theory. However, this is not true because the old findings are still cited and claimed to be correct. They are still referred to and discussed by others who think that they have a sound basis (Tomos and Leigh, 1999).

Recently, combined measurements with the pressure probe and the pressure chamber on intact transpiring maize plants have shown that both techniques yield similar values, at least for tensions of up to 1 MPa (10 bar; Wei *et al.*, 1999*a*, *b*, 2000). This was in agreement with the cohesion–tension theory. Different from the early results of the Zimmermann group, the results of Wei *et al.* showed that xylem pressure strongly and rapidly responded to changes in transpiration which is in agreement with the cohesion–tension mechanism. Most interestingly, a careful examination of the limits of the pressure probe to measure tensions showed that the equipment by itself was able to sustain tensions of up to only 1.6–1.8 MPa in short periods (Wei *et al.* 1999*a*). When the tip of the probe was positioned in the xylem, the upper limit was further reduced to about 1 MPa. So, the technique as it stands can not be used to prove or disprove the existence of tensions of up to 10 MPa (100 bar) which have been indirectly measured using the pressure chamber. Up to tensions of 1 MPa, the data were in agreement with the cohesion–tension theory. It appears that the early and present claims from the Zimmermann group are largely based on artefactual results because of limitations of the technique used. Until recently, these limitations have not been thoroughly checked for, although there had been warnings in the literature (Steudle and Heydt, 1988; Heydt and Steudle, 1991; Steudle, 1995).

With respect to the uptake of water by roots at low soil water potential the results are of crucial importance. According to the cohesion–tension theory, transpiring plants could take up water from a dry soil at a high root $Lp_r$ (as predicted by the composite transport model). On the other hand, when transpiration is switched off, root $Lp_r$ would switch to low values thus limiting water loss to the soil under these conditions.

## Transport of ABA: the root signal

The role of ABA as a long-distance stress signal produced in the root is well established. Usually, the concentration of ABA in the xylem is thought to be the signal which is carried up to the shoot with the transpiration stream. However, water uptake into the xylem would modify the signal by dilution, unless there is some apoplastic transport of ABA which could contribute to the signal. Recent measurements on excised roots of sunflower and maize indicate that this is the case (Freundl *et al.*, 1998, 2000). In sunflower and maize grown in hydroponic culture there was a significant solvent drag of ABA offered to the nutrient solution at low concentrations (0–500 nM). The effect compensated or even overcompensated for the dilution effect caused by the concomitant water uptake. It was concluded that in water-stressed plants, ABA produced in the root could be apoplastically transported across the root, at least to some extent. According to Hartung *et al.*, the biosynthesis of ABA takes place in the cytosol of all root cells (Hartung *et al.*, 1999). The strongest capacity is found in the non-vacuolated cells of root tips. According to the model of Slovik and Hartung, ABA is distributed between the apoplast and symplast according to the difference in pH between the two compartments (Slovik and Hartung, 1992). A more alkaline (less acidic) pH of the apoplast would increase the ABA concentration in the apoplast and, hence, intensify the solvent drag of ABA to the shoot with the transpiration stream. The water flow across the plant would be directly linked to the signal of ABA which is produced in the root during water stress.

In accordance with these findings was the fact that the reflection coefficient of ABA (calculated from solvent drag) was close to unity at high pH (all ABA in anionic form) and low at low pH, where a considerable amount was present as undissociated acid. When maize roots were grown in aeroponic culture and developed an exodermis, both the transport of ABA and the water flow were reduced which resulted in a concentration of ABA similar to that found in the absence of an exodermis (Freundl *et al.*, 2000). Hence, the size of the signal did not change much. It was concluded that the apoplastic passage of ABA may be significant during the signalling of water deficits from the root to the shoot. There were big differences between the two species used in that the apoplastic component was much larger in maize as compared with sunflower. The differences may be due to differences in the fine structure of the roots of the two species, namely, in the ultrafiltration properties of the endodermis. At the endodermis, there should be concentration polarization effects which may contribute to the rather high solvent drag and the low apparent reflection coefficients of ABA.

It is interesting that ABA also increased the hydraulic conductivity of maize both at the level of individual cells ($Lp$) and entire roots ($Lp_r$), perhaps, by affecting water channels (Hose *et al.*, 2000). Tests with other hormones and ABA derivates have shown that the effects on $Lp$ and $Lp_r$ are specific for the undissociated (+)-*cis-trans*-ABA. Effects were much stronger at the cell than at the root level. At the root level, $Lp_r$ did not change in the presence of a hydraulic water flow, when the apoplastic component was dominating. This is in accordance with the composite transport model. The results show that water flow (transpiration) which is usually thought to be regulated with the aid of the stress hormone ABA at the level of stomata, may interact with the ABA signal coming from the root. On the other hand, ABA may regulate water uptake under non-transpiring conditions, i.e. under conditions of water shortage. It may be speculated that, under these conditions, the cell-to-cell component of water flow is increased by an activation of water channel activity.

## Conclusions

From transport and anatomical studies it is concluded that the composite structure of roots plays an important role during the regulation of water uptake. The composite structure of roots results in composite transport of water and solutes. There is a switching between the cell-to-cell (aquaporins) and the apoplastic path which is thought to cause most of the variability of the hydraulic conductance of plant roots. The switching between transport models depends on the forces acting in the system in the presence and absence of transpiration ('hydraulic' and 'osmotic' modes of water flow). In the presence of high transpiration, the force driving water across the root will be the hydrostatic pressure difference between root medium and xylem. This allows both the apoplastic and cell-to-cell pathways to be used, even in the exo- and endodermis. When transpiration is switched off, the cell-to-cell passage is left which has a high hydraulic resistance. There is a coarse adjustment of root $Lp_r$ which is purely physical in nature and has no equivalent in the shoot. Provided that there is sufficient transpiration, the switching to hydraulic water flow provides access of the plant to soil water at low water potential. In the absence of transpiration root $Lp_r$ becomes small. This minimizes water losses to the dry soil. For plants growing at water deficits, root growth is slowed down and there are considerable apoplastic barriers blocking the hydraulic route. Under these conditions, root $Lp_r$ may be low and could be regulated along the cell-to-cell path by an opening or closing of water channels. Water channel activity has been shown to exist in root cortical cells including the endodermis. The activity of water channels may be inhibited by heavy metals, hypoxia, nutrient deficiency, low temperature, and high salinity. Measurements of inhibition at the cell and overall root $Lp_r$ are in agreement with predictions from the composite transport model.

In young roots of maize, there is a correlation between the chemical composition of apoplastic barriers and root $Lp_r$. Aliphatic suberin appears to act as the hydrophobic material which blocks the water flow across Casparian bands. Compared with the water, the solute (nutrient) permeability of roots is low. Nutrient ions once taken up are retained in the xylem and do not leak back. There is an apoplastic component of ABA transport in roots which contributes to the stress signal in the xylem (apoplastic flow of ABA). The stress signal in the xylem depends on the intensity of the rate of transpiration. The flow of ABA is affected by the presence of apoplastic barriers (exodermis). At least to some extent, ABA produced in the root during water stress, will be delivered to the apoplast and then taken to the shoot with the transpiration stream. On the other hand, ABA increases the water permeability of root cell membranes and the osmotic hydraulic conductivity of whole roots as shown by measurements with the cell and root pressure probe. These results are in line with the composite transport model. Nutrient stresses reduce water channel activity and overall root $Lp_r$. In *Lotus* roots, the diurnal rhythm of root $Lp_r$ correlated with the expression of mRNA encoding for water channels, but not with a rhythm in the *Lp* of cortical cells. It was concluded that regulation took place in the endodermis and/or stele.

In the composite transport model, the cohesion–tension mechanism of the ascent of sap plays an important role. At high rates of transpiration and tensions in the root xylem, the preferred apoplastic path for water provides a sufficient supply of shoots with water even under conditions of water shortage (hydraulic mode of water flow). The cohesion–tension mechanism has been questioned. Direct measurements of xylem pressure in leaves of intact transpiring maize plants now show that the cohesion–tension mechanism is valid, at least for a range of tensions of up to 1 MPa (10 bar).

Future work should concentrate on a more detailed mapping of hydraulic resistances in the root cylinder and how they would change in response to water shortage and other stresses. Namely, the hydraulic resistances of the exo- and endodermis and of stelar cells should be known for modelling water flow across roots. This can be done by combined measurements with the cell and root pressure probe and by measuring the propagation of changes in water potential (turgor) across the root cylinder.

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