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How does water get through roots?

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Abstract

On the basis of recent results with young primary maize roots, a model is proposed for the movement of water across roots. It is shown how the complex, 'composite anatomical structure' of roots results in a 'composite transport' of both water and solutes. Parallel apoplastic, symplastic and transcellular pathways play an important role during the passage of water across the different tissues. These are arranged in series within the root cylinder (epidermis, exodermis, central cortex, endodermis, pericycle stelar parenchyma, and tracheary elements). The contribution of these structures to the root's overall radial hydraulic resistance is examined. It is shown that as soon as early metaxylem vessels mature, the axial (longitudinal) hydraulic resistance within the xylem is usually not rate-limiting. According to the model, there is a rapid exchange of water between parallel radial pathways because, in contrast to solutes such as nutrient ions, water permeates cell membranes readily. The roles of apoplastic barriers (Casparian bands and suberin lamellae) in the root's endo- and exodermis are discussed. The model allows for special characteristics of roots 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 indicate some apoplastic by-passes for water within the root cylinder. For a given root, the model explains the large variability in the hydraulic resistance in terms of a dependence of hydraulic conductivity on the nature and intensity of the driving forces involved to move water. By switching the apoplastic path on or off, the model allows for a regulation of water uptake according to the demands from the shoot. At high rates of transpiration, the apoplastic path will be partially used and the hydraulic resistance of the root will be low, allowing for a rapid uptake of water. On the contrary, at low rates of transpiration such as during the night or during stress conditions (drought, high salinity, nutrient deprivation), the apoplastic path will be less used and the hydraulic resistance will be high. The role of water channels (aquaporins) in the transcellular path is in the fine adjustment of water flow or in the regulation of uptake in older, suberized parts of plant roots lacking a substantial apoplastic component. The composite transport model explains how plants are designed to optimize water uptake according to demands from the shoot and how external factors may influence water passage across roots.

Key words: Composite transport model, endodermis, exodermis, hydraulic conductivity, reflection coefficient, root, water, water channels.

Introduction

One of the essential functions of roots is to supply the shoot with water from the soil. The process of water movement through roots is very different from that of ions which, in most cases, involves active pumping across the plasma membrane into the cytoplasm of cells. Under conditions of transpiration, roots do not 'take up water' so much as they allow it to pass through them. In other words, water is not taken up actively, but instead moves passively through the root in response to a water potential gradient set up by transpiration. The anatomical complexity of the root dictates that the flow of water through it will also be complex. This flow is best described by a composite transport model which allows for differences in movement through individual cells, as well as through various tissues (Steudle *et al.*, 1993; Steudle, 1994*a*, *b*, 1997; Steudle and Frensch, 1996). In this review, the salient anatomical features of roots and what is known

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about their effect on the passage of water are discussed first. Molecular features, such as the presence of aquaporins in cell membranes, will also be considered. The composite model of water transport will be explained, as well as some unusual features of water and solute flow resulting from the complexity of the root.

Root anatomy underlies transport processes

The physical properties of roots are related to their anatomy and there is no way to interpret root transport data without sufficient knowledge of their structure. An immediate complicating factor is that roots are highly variable. Major differences are seen among species, habitats, and even along the length of an individual root. Common examples of such differences are the formation of aerenchyma, the development of the endo- and exodermis (with their Casparian bands, suberin lamellae, and thickened, modified walls), death of the epidermis and in some cases the entire central cortex, development of lateral roots, and production of bark. This means that results obtained with one experimental system cannot be automatically applied to all roots, and that someone who wishes to understand transport events at the cellular level must know the anatomy of his/her own plant(s).

In this review the focus will largely be on results obtained with primary roots of young maize seedlings grown in hydroponic culture (Peterson and Steudle, 1993; Peterson et al., 1993; Steudle *et al.*, 1993). Such roots are characterized by having a living epidermis and central cortex, an immature exodermis, mature proto- and early metaxylem, immature late metaxylem (i.e. with vessels still having end walls and living cytoplasm), and an endodermis with Casparian bands, but no suberin lamellae or thickened walls (Fig. 1A). At the tip of the root where the early metaxylem is immature, there is an hydraulically isolated zone (Steudle and Frensch, 1989; Azaizeh and Steudle, 1991). This part can be ignored in a consideration of water flow into the vascular tissue and thence to the shoot. The reason for the apparent non-contribution of the mature protoxylem is unknown.

Ohm's law analogy of water flow

In 1948, van den Honert introduced the idea that water movement in plants is analogous to electricity flow. He viewed the flow of water as a catenary process where each catena element is an hydraulic resistor. According to basic laws of electricity (Ohm's and Kirchhoff's laws), when components of a circuit are arranged in series, their resistances are additive, and when components are arranged in parallel, their conductances (the inverse of their resistances) are additive. There is now considerable evidence that the catenary hypothesis holds for plants (Zimmermann, 1983; Tyree, 1997). Thus, in the root cylinder the water potential will drop along the different tissues which are arranged in series (epidermis, cortex, pericyclic parenchyma, tracheary element walls). If the endodermis, for example, represents the highest resistance in the system, the drop in water potential would be the highest there. If an exodermis is formed and its Casparian bands and suberin lamellae increase its hydraulic resistance, there would be a significant drop in water potential there, too. The analogy with electrical circuits holds both on the 'micoscopic scale' (when comparing pathways for water across cells within a tissue) and at a 'macroscopic' level (when, for example, comparing different zones along roots).

Forces and flows: the nature of water movement in roots

Often the uptake of water by roots has been regarded as a simple osmotic process in which root membranes play the important role (Kramer and Boyer, 1995). Hydraulic resistances involved are usually thought to be constant. Usually it is assumed that the driving force is the gradient in water potential between soil and root xylem. However, evidence collected during the past decade indicates that this treatment has to be modified. Water movement from the soil solution into the root xylem and then up into the shoot can be treated as fluid flow through a complex structure with variable hydraulic resistances some of which are arranged in series (such as the different tissues in the root cylinder) and others of which are in parallel (such as the different cellular pathways for water). Along these paths, there are purely hydraulic processes involved such as the flow across the porous walls of cells or across the walls of tracheary elements (vessels and tracheids). Hydraulic flows are driven by hydrostatic gradients. There are also osmotic flows driven by gradients in osmotic pressure. These only occur in the presence of membranes and, besides hydraulic flow, are important whenever water moves across the membranes of cells. Osmotic water flow will be negligible in the apoplast (see the section on the radial pathways across parenchyma), because this structure will not select between water and solutes, i.e. the reflection coefficient of the apoplast will be very close to zero. Therefore, the usual textbook notion that the overall driving force for water is the gradient in water potential has to be viewed with caution. The osmotic component of water potential (the osmotic pressure, π) has to be modified by the root reflection coefficient (σ_{sr}; subscript 's' stands for 'solute' and subscript 'r' for 'root') which is a figure between zero (osmotic barrier has no selective properties at all) and unity (solutes are completely retained by the barrier). If the reflection coefficient is considered, the 'effective' osmotic component of water potential which drives the flow across the root, is $\sigma_{sr}\Delta\pi$, where $\Delta\pi$ is the osmotic pressure difference between root xylem and soil solution. Since σ_{sr} is usually smaller than unity, $\sigma_{sr}\Delta\pi$ will be smaller than expected for a semipermeable barrier. The reflection coefficient denotes the passive selectivity of a membrane or barrier. It is a measure of interactions between solute and water within a membrane or barrier. The meaning of the reflection coefficient is, therefore, different from that of the permeability coefficient.

When water moves into a root, there will be an hydraulic water flow across the apoplast, and a parallel flow across the cells (protoplasts) which would have both an hydraulic and an osmotic component. Both flows will interact with each other while water is moving radially into the root. This is so because cell membranes are highly permeable to water and water potential gradients between compartments are rapidly equilibrated. In fact, there will be nearly local water flow equilibrium between the pathways (Steudle, 1994*a*, *b*; Steudle and Frensch, 1996). In addition to the water, solutes move along both the apoplast and the cell-to-cell path (see the section on the radial pathways through parenchyma). Solutes in the apoplast move by diffusion and solvent-drag with the water whereas in the cell-to-cell path, their movement is rate-limited by the passive or active permeation across the plasma membrane. Solute movement has consequences for the water inasmuch as the solute flow changes gradients in osmotic pressure within and across the root. Thus, water flow is coupled to solute flow and vice versa. In a transpiring plant, interactions between solute and water flows will not be too important because the hydrostatic gradient will usually be the dominating force. However, at low rates of transpiration, it can be important, i.e. during the night or during water shortage. Under these conditions, phenomena such as root pressure or guttation can be seen.

Besides the radial component of water flow just discussed, there is also an axial component within the lumena of tracheary elements. This is purely a bulk flow which is propelled by hydrostatic gradients set up by transpiration. In the root, the xylem acts as a duct which collects the water taken up radially and rapidly transfers it to the shoot. This, however, requires that the axial hydraulic conductance is much larger than that of the radial pathway across the root cylinder (see below).

Along a developing root, the relative contribution of hydraulic and osmotic flow may change, namely, when apoplastic barriers are formed which interrupt the flow around root protoplasts in the endo- and exodermis (Frensch *et al.*, 1996). The composite structure of roots allows for something special which would be hard to obtain with a homogeneous membrane (such as a single cell membrane), namely, a fairly high and adjustable water permeability in the presence of a pronounced ability to retain nutrient salts transferred into the xylem. This is possible by means of a composite osmotic barrier. However, the axial and radial components of water flow will first be looked at in more detail. The axial flow component will be considered initially.

Water flow within tracheary element lumena

Vascular plants have evolved two types of highly modified cells, tracheids and vessel members, strands of which provide an axial pathway with an exceedingly low resistance to water flow. In the case of tracheids, this is accomplished by an elongate cell shape (reducing the number of end walls encountered along the axial path), loss of protoplasts, and in some species degradation of primary wall material in pits intervening between adjacent elements. In the case of vessel members, there is a similar loss of the protoplast and also a partial or complete removal of end walls between axially adjacent cells. The importance of removal of the protoplasts for reduction of the resistance to water flow can be demonstrated both theoretically and experimentally. The consequences of leaving only one intact membrane in a vessel (the tube formed by interconnected vessel members) is considered. Typical early metaxylem vessels of maize roots have a diameter of $2r = 23\ \mu\text{m}$ and thus, according to Poiseuille's law, would have a hydraulic resistance of 1.4×10^{11} MPa s m^{-3} per metre length of a vessel. A typical, measured, hydraulic conductivity of a maize root cortical cell membrane is $Lp = 7 \times 10^{-7}\ \text{m s}^{-1}\ \text{MPa}^{-1}$ (Zhu and Steudle, 1991). From this value, the resistance of a piece of membrane corresponding to the cross-sectional area of the vessel would be $1/(Lp \times \pi r^2) = 3.4 \times 10^{15}$ MPa s m^{-3}. This is larger by orders of magnitude than that of the open vessel. In other words, just one membrane patch has a resistance equivalent to that of a cylindrical vessel of a length of $(3.4 \times 10^{15})/(1.4 \times 10^{11})$ metres = 24 km! Even if it is assumed that axial water flow in tracheary elements deviates from that predicted by Poiseuille's law and would (largely because of the effects of cross walls), range between 25% of the theoretical value for tracheids and 100% for long vessels (Zimmermann and Brown, 1971), the effects of removal of membranes on the axial resistance still remain enormous.

According to Poiseuille's law, the diameter of the conducting channel has a huge effect on its hydraulic conductance (which varies with its fourth power). The diameters of various classes of vessels can be strikingly different in roots. For example in maize, narrow-diameter (5–10 μm) protoxylem vessels mature near the root tip. Then, about 25 mm from the tip, other cells in the procambial strand mature into wider, early metaxylem vessels (mean diameter: 23 μm). Finally, at distances of greater than 250 mm from the tip (depending on the growth conditions) the late metaxylem elements mature (diameter about 100 μm). Because of their diameter, vessels of the late metaxylem should be much more conductive than those of the early metaxylem. This large difference led St Aubin *et al.* (1986) to speculate that maturation of the late metaxylem would be of overriding importance for the supply of water to the shoot and that, consequently, the younger part of the root serviced only by the early metaxylem would then contribute little water (or ions) to the shoot. However, in the intact root, it is the radial rather than the axial resistances which limit water uptake. For maize roots, this can be illustrated by a rough comparison of the radial resistances with those of both the early and late metaxylem. A typical figure for the radial resistance of a 100 mm long young maize root of diameter 1 mm may be calculated from its measured radial hydraulic conductivity of 1×10^{-7} m s^{-1} MPa^{-1} (Steudle *et al.*, 1987) and root surface area. This resistance is 3×10^{10} MPa s m^{-3}. This is the minimum expected value, since these measurements were made on roots with an immature exodermis and no suberin lamellae in the endodermis. If the early metaxylem system is considered, and a length is assumed of 100 mm of this path which consists of 14 vessels with a mean diameter of 23 μm, then from Poiseuille's law a resistance of 1×10^{9} MPa s m^{-3} is calculated. This is smaller by 1–2 orders of magnitude than that for the radial flow and, therefore, the latter should limit uptake.

For the mature late metaxylem there would be 7 vessels of a diameter of 100 μm. Again, assuming a length of 100 mm, a resistance of 6×10^{6} MPa s m^{-3} is calculated which is smaller by 2–3 orders of magnitude than that of the early metaxylem and smaller by 4 orders of magnitude than that for the radial uptake. Essentially, the relations will not change when a somewhat longer zone for water uptake or longer distances of axial transport are assumed. It will also not change when more sophisticated calculations are made which assume that water is continuously taken up along the root and transported to the shoot rather than assuming that the resistances for radial uptake and for the transport in the early and late metaxylem are simply arranged in series (as done here for the sake of simplicity; Landsberg and Fowkes, 1978; Frensch and Steudle, 1989; Melchior and Steudle, 1993). In young maize roots lacking mature metaxylem, the rate-limitation of water uptake by radial water flow across the root cylinder has also been directly demonstrated experimentally in root pressure probe experiments by measuring intact roots and then removing the tip so that mature vessels of the early metaxylem were cut open. The experiments showed that rates of water exchange across the roots drastically increased after cutting (Steudle and Jeschke, 1983; Frensch and Steudle, 1989; Melchior and Steudle, 1993). The above comparison shows that regardless of the greater conductance of the late compared to that of the early metaxylem, the greatest resistance in the intact system lies in the radial path. Furthermore, the axial hydraulic conductance provided by the early metaxylem is more than sufficient to transport water to the shoot. Therefore, those parts of the root in which there are no mature late metaxylem vessels are by no means hydraulically isolated from the rest of the plant.

It is interesting that, from Poisseuille's law, the conductance of one mature vessel of late metaxylem of a diameter of 100 μm is equivalent to 357 vessels of early metaxylem (diameter: 23 μm). The maturation of the late metaxylem is advantageous in older root systems, where water from many lateral roots converges in the xylem of the main root. But, as shown above, this does not mean that axial transport becomes rate-limiting in any part of the root as long as the vessels of the early metaxylem are functioning.

Radial water flow across roots

In this section, the flow of water through the parts of the root arranged in series will be considered, with the aim of locating the major resistances in the roots. As shown above, it is these resistances which will ultimately control the flow of water through the organ. In the young maize root, the series of parts are: the epidermis, the immature exodermis and central cortex, the endodermis, the pericycle and possibly some stelar parenchyma, and the walls of the vessel members. For ease of explanation, these parts will be considered in reverse order.

Vessel walls

It is obvious that water moving in the radial path must go through the vessel wall before entering its lumen. The wall is thickened and lignin displaces the water in at least some of its intermicrofibrillar spaces. Vessel walls are not evenly thickened. Some thin, unlignified areas called pit membranes remain. In maize roots, pit membranes have a diameter of about 2 μm and occupy 14% of the total surface area of the early metaxylem vessels (Peterson and Steudle, 1993). Pits consist of primary wall and a middle lamella. It is generally assumed that most of the water passes through pit membranes and not through the thickened, lignified portion of the wall on its way to the lumen. The area available for water flow across vessels would be relatively small and this passage could represent a considerable resistance. The contribution of vessel walls as a whole to the resistance of water transport in the radial path was estimated by measuring the hydraulic resistance of the root before and after killing the surrounding living cells by heat in a specific area of the root (Peterson and Steudle, 1993). From the resulting increase in hydraulic conductance (decrease in resistance), it was concluded that vessel walls contribute from 10–30% of the resistance to water movement in the radial direction. This is not negligible. However, the majority (70–90%) of the resistance was in the living tissue located between the ambient solution and the vessel.

It is important to note that in the maize root, vessels had simple pits (with no overarching walls) and that the pit membranes occupied 14% of the wall surface. There is much variation in tracheary element wall structure, and many walls could well have lower resistances than those of the vessels we measured. For example, bordered pits allow a large area of pit membrane. Other types of thickenings, e.g. spiral and annular, also increase the relative area of primary, unlignified wall. In these cases, a higher proportion of the resistance would be found elsewhere in the tissue.

Radial pathways through parenchyma

Before considering water flow in the remainder of the radial path, most of which consists of parenchyma tissue, it is necessary to consider the cellular aspects of water flow through such a group of cells. According to Münch (1930), the part of the plant outside the plasma membrane of the living cells is termed apoplast. It includes cell walls, intercellular spaces, and the lumena of tracheary elements. The symplast, on the other hand, is the continuum of cytoplasm interconnected by plasmodesmata and excluding the vacuoles. Hence, the terms 'apoplastic' and 'symplastic' transport refer to movements within the two compartments just defined. This may be a reasonable and sufficient description for ions, but it definitely does not hold for water. The simple reason is that water moves across membranes by several orders of magnitude more rapidly than ions. So, a third path for water flow must be considered, i.e. the one in which water crosses membranes to get from one cell to the next. In a tissue, two plasma membranes would have to be crossed per cell layer as well as the short distance of wall space between adjacent cells which is usually not rate-limiting. As a result, there would be three main pathways for water flow in a tissue (Fig. 2). There could be, of course, 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 etc. These combinations could, however, be included in a model for water transport as long as allowance is made for a rapid exchange of water between pathways (Molz and Ikenberry, 1974; Molz and Ferrier, 1982; Westgate and Steudle, 1985; Steudle, 1989, 1992, 1994*a, b*; Steudle and Frensch, 1996).

In principle, the vacuole would be an additional compartment (besides the apoplast and the protoplasts depicted so far) and it could be included in the model. However, since the tonoplast usually has a low hydraulic resistance (Kiyosawa and Tazawa, 1977; Maurel *et al.*, 1997; Niemietz and Tyerman, 1997) and, in any case, could be easily circumvented by water flowing along the cytoplasm, further refinement of the model by introducing the vacuole is not necessary. To date, it has not been possible to obtain all the data necessary to describe an extended model which separates protoplasts into vacuolar and cytoplasmic compartments (tonoplast hydraulic conductivity and cross-sectional areas). Currently, it is not possible to separate even the symplastic from the transcellular path (i.e. transport through plasmodesmata from that across the plasma membrane). Hence, for pragmatic reasons the symplastic and transcellular pathways have to be considered as a cell-to-cell pathway. So, there are two parallel pathways for tissue water, the apoplastic and cell-to-cell path. Experimentally, the contribution of the cell-to-cell component can be directly obtained from measurements with the cell pressure probe (Steudle, 1993). The apoplastic component (the hydraulic conductivity of the cell wall material) is usually obtained by difference, i.e. by subtracting the hydraulic conductivity of the cell-to-cell path from that of the whole root (Zhu and Steudle, 1991).

Endodermis and exodermis

In the root, the apoplast of the endodermis is modified by the presence of a Casparian band. This structure consists of a deposit of suberin and/or lignin in the intermicrofibrillar spaces in the cell wall (Schreiber *et al.*, 1994; Schreiber, 1996; Zeier and Schreiber, 1998). It is located specifically in the radial (Fig. 1) and transverse (end) walls of the cells. It has been assumed that because the components of the Casparian band are hydrophobic, the movement of water through the wall will be prevented at this point. The validity of this assumption will be discussed later. If the majority of water is moving into the root in the apoplast, and the endodermal Casparian band is a major barrier to its movement, then injuring the endodermis should significantly decrease the resistance of the root to water flow. To test this hypothesis, a maize root was fixed on to a root pressure probe and measurements made of its hydraulic conductivity as described by Steudle (1993). A glass tube was then driven into the root so that its endodermis was injured and the hydraulic conductivity was remeasured (Peterson *et al.*, 1993; Steudle *et al.*, 1993). There was no detectable increase in hydraulic conductivity after injuring the endodermis, so the conclusion must be that the endodermis (with Casparian bands only) is not a major barrier to water movement into the root. Water flow must be going through membranes and cell walls of living cells on the radial path and the hydraulic resistance of the root is more evenly distributed within the root cylinder.

The Casparian band would not affect the radial cell-to-cell flow of water, but suberin lamellae, which occur on the tangential as well as the radial and transverse walls, could do so. Then there would be hydrophobic material laid down in the transcellular water path. Formation of the exodermis, with its Casparian bands and suberin lamellae, may also add to the overall resistance to water flow. When it is considered that in some roots, both layers can develop thickened walls which may be suberized and/or lignified (endodermis in Fig. 1B,C), there is the possibility of substantial increases in hydraulic resistance. However, results from experimental tests of these ideas have been variable. Some experiments indicate that the development of suberin lamellae in the endodermis increases the resistance to water movement (Robards *et al.*, 1973; North and Nobel, 1991), but Sanderson (1983) suggested that the development of suberin lamellae actually decreased the resistance and that development of the thickened wall increased it. A study of hydraulic conductivity in maize roots with suberin lamellae in the endodermis and exodermis failed to show any correlation (Clarkson *et al.*, 1987). On the other hand, measurements of the hydraulic conductivity of onion roots indicated an increased resistance in basal zones which had developed suberin lamellae in the endodermis, and Casparian bands and suberin lamellae in the exodermis (Melchior and Steudle, 1993). An exodermis is usually absent in young maize roots grown in hydroponics. However, it can be induced by growing seedlings in aeroponics (mist chamber; Zimmermann and Steudle, 1998). The latter roots had a greater resistance to water flow than the former as measured with a pressure chamber (steady water flow). This suggests that the exodermis, when present, is a substantial barrier to water flow.

The movement of water in the apoplast cannot be quantified by the movement of apoplastic dyes. For example, in the experiments of Zimmermann and Steudle (1998), the external media contained the 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 for water and this ionic compound simultaneously. 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 (subscript 'r' stands for 'root') and literature data of 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 (i) 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 PTS in the xylem. It is possible that the breakthrough of laterals across the exodermis could have

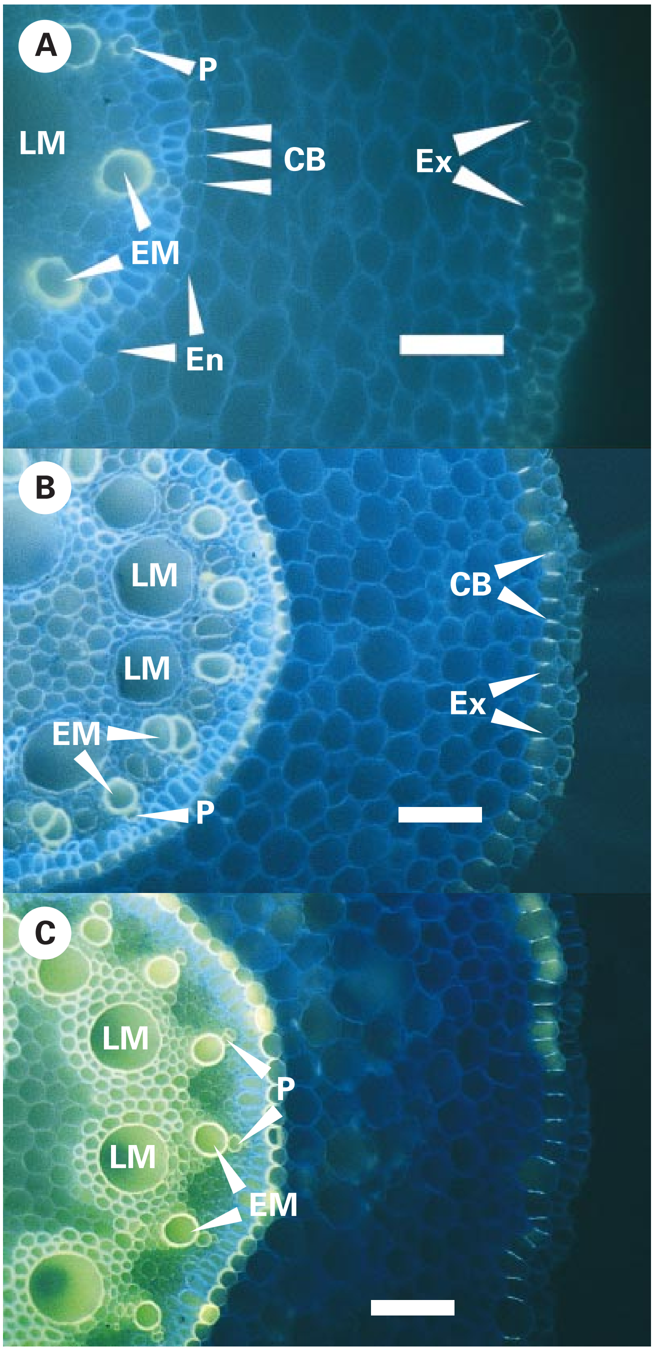
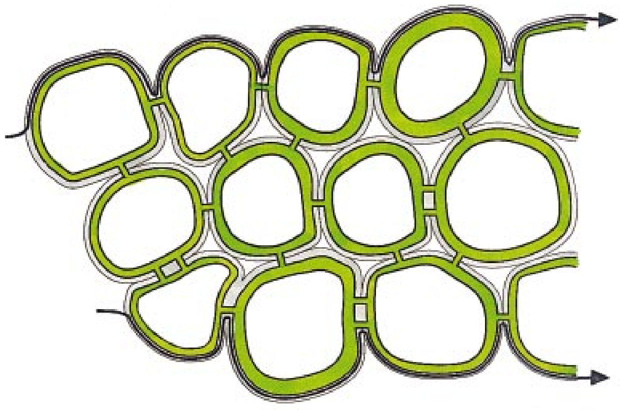


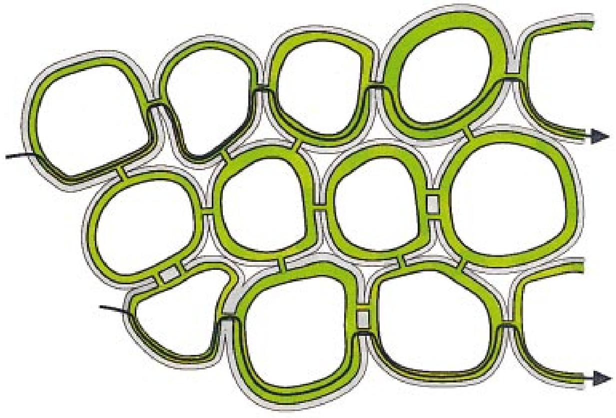
Fig. 1. Cross-sections of maize primary roots at various stages of development. Specimens were photographed under UV/violet light (wavelength = 390–420 nm) following staining with berberine and either aniline blue or toluidine blue O. Scale bars = 100 μm. (A) Immature exodermis (Ex), endodermis (En) with Casparian bands (CB), mature protoxylem (P), mature early metaxylem (EM), immature late metaxylem (LM). (B) Mature exodermis, endodermis with asymmetrically thickened walls, mature protoxylem and early metaxylem, immature late metaxylem. (C) As in (B), but late metaxylem (LM) is mature. Walls of cells surrounding the late metaxylem elements are thickened and lignified.

Routes of water flow in plant tissue

(A) Apoplastic path



(B) Symplastic path



(C) Transcelluar path

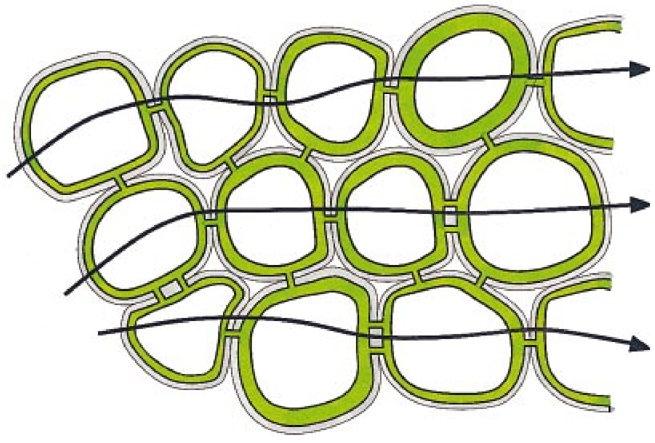


Fig. 2. Routes of water flow in plant tissue. The tissue is represented by four cell layers arranged in series. (A) Denotes the apoplastic path (cell walls, grey) around protoplasts. The symplastic path (B) is mediated by plasmodesmata which bridge the cell walls between adjacent cells so that a cytoplasmic continuum is formed (green). During the passage along the apoplast and symplast, no membranes have to be crossed. On the transcellular path (C), two plasma membranes have to be crossed per cell layer. The transcellular path is used especially by water which has a high membrane permeability. Usually, this component is negligible for solutes. Note that the symplastic and transcellular flow components cannot 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 root, the apoplastic flow component is modified by the existence of apoplastic barriers (Casparian bands, suberin lamellae). These are usually thought to be completely impermeable for water and solutes (including nutrient ions).

provided a pass for PTS across this barrier. (ii) Apoplastic dyes can not be used to trace the flow of water. This mistake has some tradition in botany (Strugger, 1939; Varney *et al.*, 1993).

The central cortex, immature exodermis and epidermis

Returning to the young maize root, the vessel walls and the endodermis without suberin lamellae have been ruled out as major resistances to water flow. Where, then, does this resistance occur? It is not in the epidermis, since when a region of this tissue was scraped away, along with a portion of the outer cortex, the hydraulic conductivity of the root remained unchanged (Peterson *et al.*, 1993). It proved technically impossible to remove large areas of the epidermis and central cortex without injuring the endodermis. However, it was possible to dissect away a wedge, comprising about one-third of the cortex, including the outer walls of the endodermis at most points. This treatment reduced the resistance to water flow approximately in proportion to the amount of tissue removed. From these results, it was concluded that, at least for the young maize roots used, the major resistance to water flow was evenly spread over the living tissues of the root (Peterson and Steudle, 1993). This is in contrast to the usual concept that in roots, the major resistance to water flow is in the endodermis.

As discussed above, the formation of suberin lamellae in both the endodermis and exodermis could result in two localized regions of high resistance for water and ion flow in the apoplast of roots. If true, this would mean that the exodermis could contribute to the regulation of water uptake into roots as suggested by experiments in which roots were grown in soil with low water potential (Cruz *et al.*, 1992; Stasovski and Peterson, 1993) or high salinity (Azaizeh *et al.*, 1992; Peyrano *et al.*, 1997). On the other hand, if the exodermis is a barrier for nutrient ions, this would mean that the cortical apoplast forms a compartment storing any nutrient ions leaking out of the cortical cells. To date, there are, for technical reasons, no quantitative values of the permeability of the exo- and endodermis of intact roots to water and ions. These direct measurements are, however, badly needed to work out the functions of the two structures. The approach of Zimmermann and Steudle (1998; see above) may be used to get this quantitative information. For water, changes in cell *Lp* could be directly obtained with the cell pressure probe. Changes in the hydraulic resistance at the tissue level may be derived from the propagation of changes in water potential (osmotic and hydrostatic pressure) across the root cylinder. The techniques for doing this are, in principle, developed (Zhu and Steudle, 1991). In the future, they will be used, namely, to see how hydraulic resistances of the exo- and endodermis would change in response to external parameters (drought, salinity, low oxygen, nutrient deprivation, etc.).

Role of the endodermis during solute uptake

The decrease in root pressure which occurred when even a few cells of the endodermis were injured was an interesting observation (Peterson *et al.*, 1993). It indicated that, unlike the situation for water, the diffusion of ions out of the stele was strongly impeded by the endodermis. However, the reduction in root pressure was very rapid which suggested that there was also a bulk flow of xylem solution across the leak which constituted a low-resistance pathway between a compartment of higher pressure (the stele) and one of lower pressure (the external medium). The result confirmed the long-assumed role of the endodermis as a barrier to the back-diffusion of ions released into the apoplast of the stele. The endodermis thus confines ions to a zone near the tracheary elements, making the delivery of ions to the shoot more efficient, and also allows root pressure to build 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.

The root is not a perfect osmometer

From the above discussion of the role of the endodermis during water and ion movement into roots (high water permeability at low solute permeability), it may be tempting to equate the root to an individual cell, which behaves like a perfect osmometer or nearly so. A perfect osmometer would be completely impermeable to solutes, i.e. would have a solute permeability coefficient of $P_s = 0$, and a reflection coefficient of $\sigma_s = 1$. However, as already mentioned, measured σ_{sr} values in whole roots are substantially smaller than unity and the root cylinder is permeable to ions. The results also showed that for the solutes usually present in roots (nutrient salts, sugars, etc.), the passive root permeability (as expressed by the root permeability coefficient, P_{sr}) was rather low. Thus, nutrients once taken up by active processes would not easily leak back to the soil solution. So, unlike individual cells, roots have a low reflection coefficient. Usually, reflection coefficients of between 0.2 and 0.8 correlate with a very high passive solute permeability. The reason for the deviation found for roots is that this relation holds for single membranes. The root, however, is an osmometer which has a complex 'composite osmotic barrier' made up of several layers of cells. In such a system, the relation between reflection and permeability coefficients are apparently different than in an individual cell (see below). Unstirred layer effects may contribute to the low root σ_{sr}, but correction for this effect did not significantly change the picture (Steudle and Frensch, 1989).

It has been proposed that the low reflection coefficients of roots are due to apoplastic by-passes in the root cylinder. These could be parts of the root where the endodermis has not yet developed a Casparian band, or of arrays where root initials are growing. It has been shown that in the latter arrays, the endodermis does not form a tight barrier (Peterson *et al.*, 1981). The question as to whether apoplastic by-passes contribute to the overall transport was investigated in great detail for young maize roots (Steudle *et al.*, 1993). Their root pressure (measured with the root pressure probe) was 0.08–0.19 MPa and the hydraulic conductivity $Lp_r = 3 \times 10^{-7}$ m s^{-1} MPa^{-1} (hydraulic water flow). Using NaCl as a test solute, it was found that the root σ_{sr} was 0.64 and solute permeability $P_{sr} = 3.8 \times 10^{-9}$ m s^{-1}. Areas for apoplastic by-passes were estimated from cross and longitudinal sections in the root tip (where no Casparian band was yet developed) and from sections made in arrays with secondary root initials. It was found that for young roots of a length of 89–174 mm, the area lacking Casparian bands was only 0.080% of the total area of the endodermis. This was rather low, but was sufficient to reduce root σ_{sr} from a value around unity to the low value measured. When the endodermis was punctured, there was no effect on root Lp_r, but root pressure decreased although it still remained substantially higher than zero (0.02–0.07 MPa) despite the leak. Effects on the root reflection coefficient and on solute permeability were most dramatic. Root σ_{sr} was decreased by one-third and root P_{sr} increased by a factor of 2–3. Roots still behaved like osmometers. They responded to hypertonic or hypotonic solutions as expected, although with a 'passive selectivity' (as expressed by the root reflection coefficient), which was lower than that before puncturing.

When the root was allowed to remain on the probe for several hours, the leakage healed (possibly by the deposition of phenolic substances), and root pressure and root σ_{sr} increased again. This area of the root is quick to heal compared to a wound in the central cortex, which may take 4 d to seal off (Moon *et al.*, 1984). In nature, roots apparently have developed mechanisms to restore the function of the endodermis rapidly following wounding.

The results obtained in the puncturing experiments are in line with those obtained during microsurgery of roots (see above; Peterson *et al.*, 1993). They demonstrate that the endodermis is an effective barrier for ions, but not so much for water, at least for the young roots used which had not yet developed suberin lamellae or thickened walls in the endodermis. The results show that roots may function even in the face of some leakage flows or apoplastic by-passes of water and low molecular weight solutes, as already suggested from the other experimental findings (see above).

Composite transport model of the root

The results from the puncturing experiments just mentioned and earlier evidence from work with root pressure probes and with other techniques have led to the composite transport model of the root which explains

- low root reflection coefficients,
- differences between osmotic and hydraulic water flow,
- differences between woody and herbaceous plants, and
- the variability in root hydraulics, i.e. that root Lp_r usually increases with water flow.

Low reflection coefficients are just explained by the existence of apoplastic by-passes in arrays where Casparian bands have not yet developed or even by some by-pass flow of water across the Casparian band itself. Recently, Schreiber (1996) and Zeier and Schreiber (1998) have analysed Casparian bands of different species. They found that lignin was a major chemical component rather than suberin (as usually thought). Since lignin is still rather hydrophilic, this would be consistent with the idea of some passage of water across Casparian bands. The puncturing experiments have shown that even small (by cross-sectional area) by-passes have a big effect on the root reflection coefficient (Steudle *et al.*, 1993). According to irreversible thermodynamics this is so because the apoplast is a path of a fairly high hydraulic conductance and very low reflection coefficients (Steudle, 1994*b*; Steudle *et al.*, 1993; Steudle and Frensch, 1996). Overall values of σ_{sr} are, thus, mixed values to which the two pathways contribute according to their hydraulic conductance. Even for solutes for which cell membranes have a $\sigma_s \approx 1$, overall root σ_{sr} is substantially smaller than unity. According to the model, there will be a circulation flow of water in the root as long as there is a concentration gradient between the xylem and root medium (Fig. 3). Recently, this circulation flow and the resulting low root σ_{sr} has also been demonstrated in computer simulations in which overall flows (water, solutes) and reflection coefficients have been calculated using measured root cell data (Melchior and Steudle, unpublished results).

In roots, differences between *hydraulic and osmotic water flow* are considerable. In herbaceous plants, they can differ by as much as an order of magnitude and, in woody plants, up to three orders of magnitude (Rüdinger *et al.*, 1994; Steudle and Meshcheryakov, 1996; Steudle and Heydt, 1997). Differences are expected from the model because, in the absence of a hydrostatic pressure gradient, the apoplastic path should be inefficient due to its very low reflection coefficient (no membranes present) and $\sigma_{sr} \cdot \Delta\pi \approx 0$. This means that only the cell-to-cell component is left for water movement. However, this can, perhaps, not solely explain the findings (Melchior and Steudle, unpublished results). It must be assumed that in the presence of a hydrostatic gradient, the wall Lp_{cw} is larger than in its absence, e.g. by a filling of some of the intercellular spaces and, hence, increasing the cross-sectional area available for apoplastic water flow (Steudle and Frensch, 1996; Steudle, 1997). So, the model can readily explain both the differences in the effect of driving forces and the *variable root* Lp_r, i.e. the finding that Lp_r increases with increasing water flow across roots. This is an important result, because the effect has been reported in the literature for more than 60 years (Brewig, 1937; Brouwer, 1954; Weatherley, 1982), but until now no convincing explanation of it has been given (Fiscus, 1975; Passioura, 1988).

Differences between herbaceous and woody species include both lower values of root σ_{sr} of the woody species and huge differences between osmotic and hydraulic flow in the latter. At least qualitatively, this is also explained by the model. Woody species have, on average, a root Lp_r which is smaller than that of roots of herbs by an order of magnitude (Rüdinger *et al.*, 1994; Steudle and Meshcheryakov, 1996; Steudle and Heydt, 1997). Hence, from the composite transport model, apoplastic by-pass flows should have a much bigger effect on the overall root σ_{sr} with these species. So, roots from woody species should have reflection coefficients which are quite low in the presence of low solute permeability as found (Table 1).

Physiological consequences of composite transport

Perhaps the most obvious consequence of composite transport in roots is that water supply to the shoot by the root may change according to the demand of the shoot. 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. 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 shortage. Under these condi-

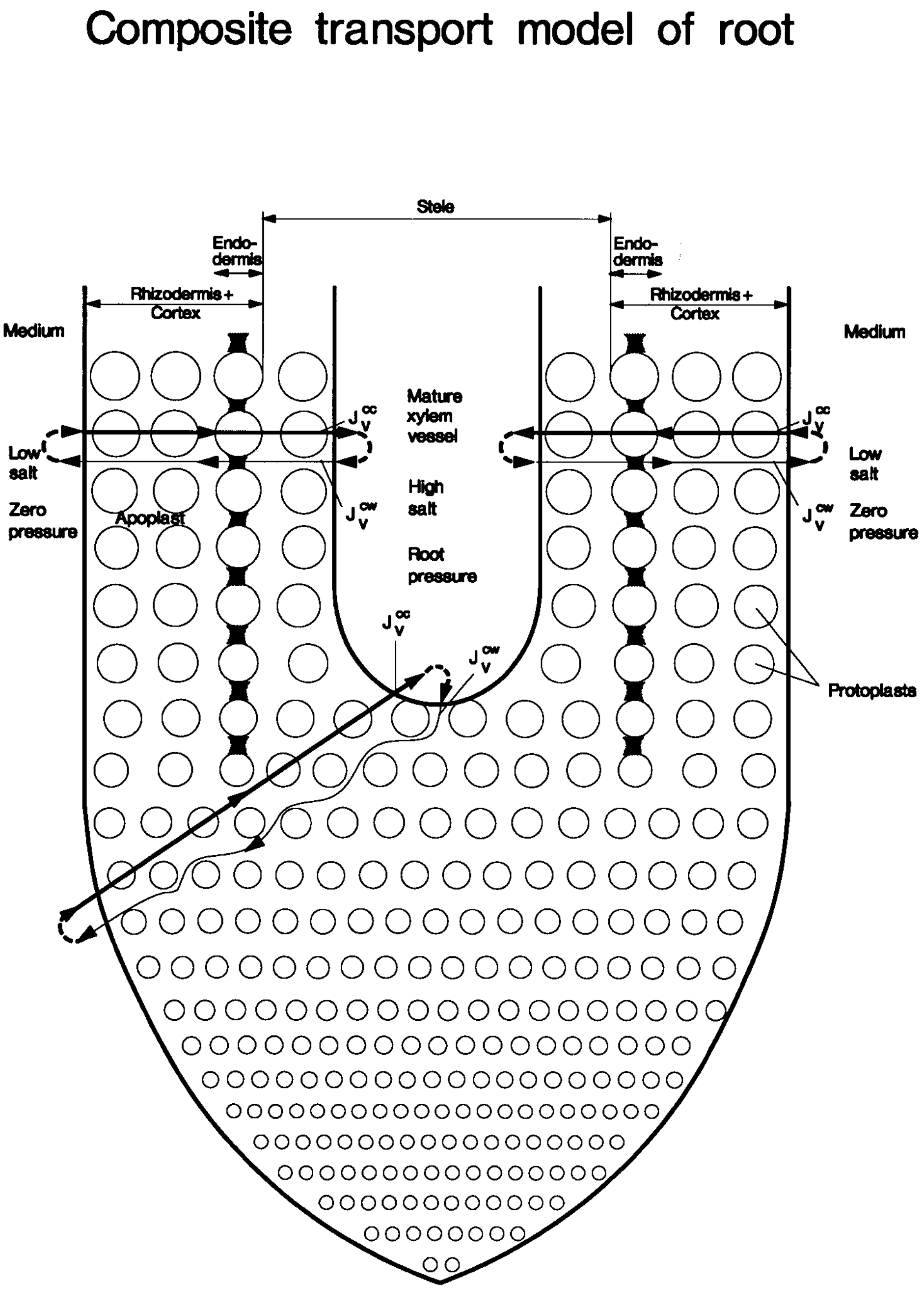


Fig. 3. Composite transport model of root (schematical). The root osmotic barrier is comprised of cells (protoplasts) and the apoplast. The apoplastic path may be interrupted by Casparian bands in the endo- and exodermis (exodermis not shown for the sake of simplicity). Water and solutes move along two parallel pathways (cell-to-cell and apoplastic routes which are denoted by superscripts 'cc' and 'cw', respectively). The cell-to-cell path has a high selectivity (reflection coefficient, $\sigma_{sr}^{cc} \approx 1$), and the apoplastic path a very low selectivity for solutes ($\sigma_{sr}^{cw} \approx 0$). At low rates of transpiration, this results in a circulation flow of water in the root (denoted by J_V) and in a low overall root σ_{sr} (as found experimentally). The model explains variable root hydraulic conductivity which depends, in part, on the nature of the driving force. For further explanation, see text.

tions, roots may be protected from excessive water loss to the soil by their high hydraulic resistance. Thus, the composite transport model provides an optimization allowing an adjustment of root hydraulics according to the demands from the shoot. The leak rate for solutes is kept low during all conditions.

The transcellular path: role of water channels

So far attention has been focused on the role of the apoplast and how barriers there would affect the radial passage of water across roots. However, the transcellular or symplastic components may be important as well. In

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. There are, to date, no data of cell *Lp* for tree roots. It can be seen that, 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. Although there is some overlapping of the data, tree root Lp_r is, on average, smaller by an order of magnitude than that of herbaceous plants. For both herbs and trees, values of root σ_{sr} are significantly lower than unity for solutes for which cell membranes exhibit a σ_s of virtually unity. For tree roots, σ_{sr} values are smaller by a factor of two than for the roots of herbs. The findings are explained by the composite transport model of the root (see text).

Species	Root $Lp_r \times 10^8$ (m s^{-1} Mpa^{-1})		Root permeability $P_{sr} \times 10^9$(m s^{-1})	Root reflection coefficient σ_{sr} (1)	Techniques	References
	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)
Triticum aestivum primary root	— Cell Lp: 12	0.5–5.5	—	—	Cell pressure probe and stop flow	(b) and (c)
Zea mays primary root	1–46 Cell Lp: 24	0.1–5	sucrose: 3.0 NaCl: 6–14	mannitol: 0.4–0.7 sucrose: 0.54 NaCl, KCl: 0.5–0.6	Cell and root pressure probe	(d) to (g)
Zea mays root system	21	2.2	—	nutrients: 0.85	Stop-flow technique and osmotic flow	(h) and (i)
Allium cepa primary root	14	0.02–2	$NaNO_3$: 0.7	KCl, mannitol, $NaNO_3$, and NH_4NO_3: 0.35–0.88	Root pressure probe	(j) and (k)
Phaseolus coccineus primary root	2–8 Cell Lp: 30–470	3–7	mannitol: 0.15 NaCl: 0.21 KCl: 0.7–0.9	mannitol: 0.68 NaCl: 0.59 KCl: 0.43–0.54	Root presure probe	(l)
Phaseolus vulgaris root system	30	0.56	nutrients: 1.3	nutrients: 0.98	Pressure chamber and osmotic flow	(h) and (m)
(B) Woody plants						
Picea abies root system	6.4	0.017	n.m.	Na_2SO_4, K_2SO_4, $Ca(NO_3)_2$: 0.18–0.28	Root pressure probe	(n)
Quercus robur root system	0.5–4.8	0.003–0.062	n.m.	mannitol: 0.19–0.43 NaCl, KCl: 0.12–0.35	Root pressure probe	(o)
Fagus sylvatica root system	0.35–1.6	0.022–0.11	n.m.	mannitol: 0.29–0.82 KCl: 0.22–0.55 NaCl: 0.32–0.64	Root pressure probe	(p)

(a) Steudle and Jeschke, 1983; (b) Jones *et al.*, 1983; (c) Jones *et al.*, 1988; (d) Steudle *et al.*, 1987; (e) Steudle and Frensch, 1989; (f) Zhu and Steudle, 1991; (g) Peterson *et al.*, 1993; (h) Newman, 1973; (i) Miller, 1985; (j) Melchior and Steudle, 1993; (k) Melchior and Steudle, 1995; (l) Steudle and Brinckmann, 1989; (m) Fiscus, 1986; (n) Rüdinger *et al.*, 1994; (o) Steudle and Meshcheryakov, 1996; (p) Steudle and Heydt, 1997.

the composite transport concept, it may even dominate depending on the conditions, i.e. in the absence of hydrostatic pressure gradients or when the passage across the apoplast is entirely blocked by Casparian bands. 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 under any conditions (Table 1). For others, the effects are quite variable. To date, there have been only a few attempts 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 ruled out. Other experiments indicate that nutrient deprivation reduces water channel activity as well (Carvajal *et al.*, 1996). For intact internodes of *Chara*, there are, to date, detailed data on the function of water channels. They demonstrate both the selectivity of water channels and their significance during overall water transport. As for animal cells, the closure of water channels had a large effect on the cell *Lp* of *Chara* which was reduced by 75% or even more (Henzler and Steudle, 1995; Tazawa *et al.*, 1996; Schütz and Tyerman, 1997). 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. However, 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). According to these results, water channels in plants do not appear to be as selective as has been sometimes proposed (Chrispeels and Maurel, 1994; Maurel, 1997; Schäffner, 1998). This is also indicated by a recent study on the temperature dependence of water and solute flow in *Chara* (Hertel and Steudle, 1997). Experiments are necessary at both root and cell levels to evaluate the effects of channel blockage on overall transport. Preliminary results on maize roots show that root behaviour is similar to that of the *Chara* internode (Henzler and Steudle, unpublished results). If true, it may be concluded that the water uptake by older parts of the root and suberized roots is governed or controlled by water channels. In younger tissue, there should be some sharing of components between pathways as predicted by the composite transport model. Thus, there may be a 'coarse adjustment' of water flow due to a 'switching' between pathways which is governed by the demand for water from the shoot (xylem tension) and is purely passive in nature. The 'fine regulation' due to the action of water channels may be under metabolic control such as the phosphorylation of channel protein (Johansson *et al.*, 1996; Maurel, 1997). During 'fine adjustment', passage cells in the endo- and exodermis may play a crucial role (Peterson and Enstone, 1996).

Conclusions

From recent anatomical and transport studies and from other work, it was concluded that the composite structure of roots plays an important role in water uptake. The composite root structure results in a composite transport for water and solutes. The parallel arrangement of the apoplastic and cell-to-cell paths, and the exchange of water between pathways is important. The composite transport model predicts large differences between hydraulic and osmotic water flow across roots as well as some variability in root hydraulic resistance as found experimentally. Composite transport gives rise to low root reflection coefficients. The variable root hydraulic conductivity allows some adjustment of water uptake by roots to the demands from the shoot which is favourable to the plant. It appears that solute relations are not really affected by the variable root Lp_r as the solute permeability remains low despite the variability in the rates of water uptake. Thus, during periods of varying water supply, roots are optimized in their abilities to use water resources in the soil. Optimization of water uptake is brought about by apoplastic by-passes which are more intensively used or 'switched on' in the presence of high rates of transpiration (hydraulic water flow) than in their absence. The formation of apoplastic barriers (Casparian bands, suberin lamellae) in the endo- and exodermis modifies the process. In addition to the adjustments along the apoplastic path, there may be responses or adaptations which change the cell-to-cell path. These could be due to changes in the activity of water channels in root cell membranes such as in the passage cells of the endo- and exodermis. To date, the contribution of this component has not been quantified by direct measurement. It is proposed that water channel activity accounts for a 'fine adjustment' of water uptake under conditions of water shortage in young roots, or when the endo- and exodermis have suberin lamellae with the exception of passage cells. Quantification of the role of water channels will require more sophisticated measurements of water flows in intact roots at the cell and root levels.

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