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Water Transport in Maize Roots[1]

MEASUREMENT OF HYDRAULIC CONDUCTIVITY, SOLUTE PERMEABILITY, AND OF REFLECTION COEFFICIENTS OF EXCISED ROOTS USING THE ROOT PRESSURE PROBE

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ABSTRACT

A root pressure probe has been used to measure the root pressure (P_r) exerted by excised main roots of young maize plants (*Zea Mays* L.). Defined gradients of hydrostatic and osmotic pressure could be set up between root xylem and medium to induce radial water flows across the root cylinder in both directions. The hydraulic conductivity of the root (Lp_r) was evaluated from root pressure relaxations. When permeating solutes were added to the medium, biphasic root pressure relaxations were observed with water and solute phases and root pressure minima (maxima) which allowed the estimation of permeability (P_{Sr}) and reflection coefficients (σ_{sr}) of roots. Reflection coefficients were: ethanol, 0.27; mannitol, 0.74; sucrose, 0.54; PEG 1000, 0.82; NaCl, 0.64; KNO_3, 0.67, and permeability coefficients (in 10^{-8} meters per second): ethanol, 4.7; sucrose, 1.6; and NaCl, 5.7. Lp_r was very different for osmotic and hydrostatic gradients. For hydrostatic gradients Lp_r was $1 \cdot 10^{-7}$ meters per second per megapascal, whereas in osmotic experiments the hydraulic conductivity was found to be an order of magnitude lower. For hydrostatic gradients, the exosmotic Lp_r was about 15% larger than the endosmotic, whereas in osmotic experiments the polarity in the water movement was reversed. These results either suggest effects of unstirred layers at the osmotic barrier in the root, an asymmetrical barrier, and/or mechanical effects. Measurements of the hydraulic conductivity of individual root cortex cells revealed an Lp similar to Lp_r (hydrostatic). It is concluded that, in the presence of external hydrostatic gradients, water moves primarily in the apoplast, whereas in the presence of osmotic gradients this component is much smaller in relation to the cell-to-cell component (symplasmic plus transcellular transport).

The hydraulic resistance of the root is an important factor in the water relations of plants. To a large extent, the root resistance will determine the water status of the shoot because, next to the stomata, the root usually offers the highest resistance to water within the soil/plant/atmosphere continuum. The hydraulic conductance of the root ($Lp_r \cdot A_r$)[3] is a rather complex parameter which depends on the root structure and anatomy as well as on the pattern by which different parts of the root contribute to the overall water transport at different stages of root development. Also, different tissues within the root cylinder (rhizodermis, cortex, endodermis, stele) may offer different resistances to the radial movement of water which has to cross several cell layers arranged in series. For each of the tissues, there are different parallel pathways, namely, the path around cells (apoplasmic path), the symplasmic pathway via plasmodesmata, and the transcellular pathway which involves a crossing of two membranes per cell layer.

It has been found that the Lp_r of plant roots depends on the absolute value of the water flow per m^2 of root surface (J_{Vr} in $m^3\ m^{-2}\ s^{-1}$) in that Lp_r increases with increasing J_{Vr} (for reviews, see Refs. 27 and 37). The dependence of Lp_r on J_{Vr} has been interpreted by dilution effects in the root xylem which suggest that the observed nonlinearity of flow and water potential is only apparent (7) or by changes in the relative contribution of apoplasmic and symplasmic transport (27). A number of observations suggest that Lp_r is also dependent on root metabolism, since inhibitors such as CCCP and KCN reduce Lp_r (28). Furthermore, plant hormones such as ABA and kinetin affect J_{Vr} and Lp_r (*e.g.* Refs. 3 and 27). Because inhibitors and hormones also influence the solute flow across the root (J_{sr}), is has been concluded that the changes in Lp_r result from an interaction between water and solute flows, although there are exceptions which show that J_{sr} may not be influenced by J_{Vr} (30). However, an ability of the plant to regulate Lp_r by controlling the membrane Lp or the resistance of the symplast cannot be completely excluded (27). At present, the question of how these different effects determine the absolute value of Lp_r cannot be answered completely, mainly because proper models of root water transport are lacking.

From physiological and ecological points of view the variations of Lp_r resulting from hydraulic properties of the root, an interaction with solute flow, and hormonal actions, are important because they could contribute to balance the various demands of the shoot for water. However, these conclusions should be cautious, because the scatter in the absolute values of Lp_r found in the literature may, in part, be due to the fact that different

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[3] Abbreviations: P_r = root pressure; P = cell turgor pressure; J_{Vr} = radial water transport across the root; Lp_r = root hydraulic conductivity; Lp = cell hydraulic conductivity; P_{sr} = permeability coefficient of root for solute 's'; σ_{sr} = reflection coefficient of root for solute 's'; ϵ_S = elastic modulus of measuring system ϵ_x = elastic modulus of xylem; V_x = volume of xylem; A_r = root surface area; C_x = solute concentration in the xylem; C_m = concentration in the medium; k_{rw} = rate constant of water exchange between root xylem and medium; k_{rs} = rate constant of solute exchange between root xylem and medium; $T^w_{r1/2}$ = half-time of water exchange between root xylem and medium; $T^s_{r1/2}$ = half-time of solute exchange between root xylem and medium; superscripts '*en*' and '*ex*' denote flows from the medium into the root xylem or from the xylem into the medium, respectively.

experimental techniques have been used for the measurement, such as simple root exudation (*e.g.* Ref. 16) or enhanced exudation by pressurizing roots (*e.g.* Refs. 8 and 19). Experiments have been performed with excised roots and with intact plants. The use of intact plants may cause problems because of the difficulty of exactly determining the driving forces for root water transport, whereas experiments with excised, pressurized root systems may be criticized because the conditions are quite different from those in the intact plant.

The root pressure probe, recently developed for measuring root water relations (32), could perhaps be used to overcome some of the difficulties. The technique uses for the measurement the root pressure naturally developed by plants. Stationary root pressures can be measured and manipulated in excised roots in order to induce water flows across the root cylinder which can then be monitored. Flows can be induced by either hydrostatic or osmotic gradients. The measurements at the organ level can be combined with those at the cell level using the cell pressure probe (17). The root pressure probe has been already applied to segments of young barley roots where the combination with cell measurements suggested a substantial contribution of the cell-to-cell pathway (symplasmic plus transcellular) to the total water transport (32).

In the following paper, we extend these measurements of root hydraulic resistances and water pathways using maize roots for which a considerable amount of data of Lp_r already exists in the literature (2, 3, 16, 21–25, 28). As for barley, measurements were performed on the organ and cell level in order to get a more detailed insight into transport mechanisms. Furthermore, the root pressure probe technique has been extended to allow the measurement of interacting solute transport. Passive solute permeation (permeability coefficients) and reflection coefficients are determined in the same experiment along with the root pressure measurements.

MATERIALS AND METHODS

Plant Material. Maize seeds (*Zea mays* L. cv B73 × Mo17) were treated with 1% NaOCl solution and thoroughly rinsed with distilled water. They were then stored in the dark on filter paper soaked with 0.5 mM $CaSO_4$ solution at 23°C for 2 to 3 d for germination. In order to induce the development of the root system the seedlings were planted on vermiculite also soaked with 0.5 mM $CaSO_4$ for another 2 to 3 d period before they were transferred to hydroculture. The medium ('Johnson-solution' as modified by Epstein [6]) contained (in mM): 1.5 KNO_3, 1.0 $Ca(NO_3)_2$, 0.5 $NH_4H_2PO_4$, 0.25 $MgSO_4$ along with a micronutrient solution. The plants used for the experiments ranged in age between 5 and 13 d. The root systems were 89 to 340 mm long. In root pressure probe experiments, end segments of the main root were used which were excised at a length of 45 to 128 mm. Main roots of this length should already contain different developmental states of the endodermis (primary, secondary, and tertiary endodermis). The segments varied in diameter from 0.7 to 1.2 mm. For some end segments of the main roots, the cell dimensions were also estimated under the microscope from longitudinal and cross sections, approximating the cells as cylinders. These data were used to evaluate water relations parameters of individual root cells (hydraulic conductivity, Lp, and volumetric elastic modulus, ε) at different positions within the root cortex (see below) by combining the data. At a distance of 25 to 50 mm from the root apex and a depth from the root surface to 300 μm, the diameters of the cortical cells ranged between 26 and 43 μm and the lengths between 205 and 305 μm. The diameters of epidermal cells were about half of those of the cortical cells. The volume of the root xylem was also estimated from cross sections of the roots at different positions. The xylem volume ranged between 8.7 and 15.9% of the total volume of the excised roots with an average at 12.3%.

Measurement of Root Pressure (P_r) and of Hydraulic Conductivity (Lp_r) of Root Segments. P_r and Lp_r were measured in a way similar to that previously described for barley roots (32). The root segments were tightly connected with the root pressure probe inserting them through a silicone seal (Fig. 1). The cylindrical seal was prepared from liquid silicone material (Xantopren plus from Bayer, Leverkusen, FRG). The inner diameter of the seal was adapted to the diameter of individual root segments. This type of seal fulfilled the necessary requirements of being water-tight even at pressures of several bars and, at the same time, not interrupting the water flow across the xylem nor damaging the root and causing leaks.

The root pressure probe was, in principle, similar to the pressure probe used for giant algal cells (*cf.* Ref. 33). It consisted of a pressure chamber filled with silicone oil to which a capillary was attached with an internal diameter of 200 μm (Fig. 1). The microcapillary was connected on the other side with the seal for the root segment. A pressure transducer within the chamber continuously measured P_r. The chamber and part of the microcapillary were filled with silicone oil, whereas the rest was filled with distilled water (or 0.5 mM $CaSO_4$ solution) so that a meniscus formed between oil and water within the capillary. This meniscus served as a reference during the measurements and could be followed under the microscope. The whole system was filled first with water and oil without any air bubbles and was then connected with the excised root. Under these conditions, the P_r developed by the segment could be measured. Stationary root pressures (P_{ro}) were usually obtained after a period of 1 to 2 h after fixing the root to the probe. Root pressures of individual roots could be recorded for several hours.

The compressibility of the measuring system (volume, V_S; see Fig. 1) is an important factor for the measurements. This parameter is given by the elastic modulus of the system ($\varepsilon_S = V_S \cdot \Delta P_r / \Delta V_S$; see also Appendix A) or by $\Delta V_S / \Delta P_r$ which is the directly measurable quantity. $\Delta V_S / \Delta P_r$ was obtained by completely clos-

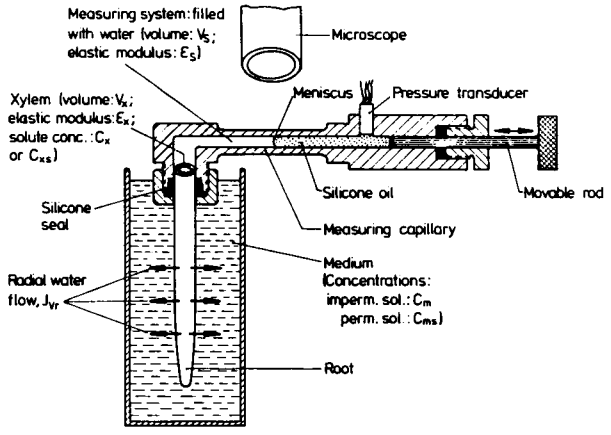

FIG. 1. Root pressure probe for measuring water flows (J_{Vr}) and hydraulic conductivity (Lp_r) of excised roots (schematical). The root is connected to the apparatus by a pressure-tight silicone seal so that a stationary root pressure (P_{ro}) is developed in the system by exudation. This pressure can be manipulated by changing the internal volume of the system with the aid of a movable rod (hydrostatic experiments) or by changing the osmotic pressure of the medium (osmotic experiments). Changes result in hydrostatic or osmotic relaxations (Figs. 2 and 3). Root pressures are recorded by a pressure transducer. When the apparatus is filled with silicone oil and water, a meniscus forms between the two liquids within the measuring capillary. This meniscus serves as a reference point during the measurements. Movements of the meniscus can be followed by a stereomicroscope and defined changes of the volume of the measuring system can be produced in order to quantify radial water flows (J_{Vr}) across the root. For further explanations see text.

ing the seal which usually contains the root and changing V_S with the aid of the metal rod of the root pressure probe (see peaks in the traces in Figs. 2 and 3). The lower the absolute value of $\Delta V_S/\Delta P_r$ the higher is the sensitivity by which water movements across the root can be measured. $\Delta V_S/\Delta P_r$ ranged from 0.14 to 0.011 $\mu l \cdot bar^{-1}$ (0.14 to 0.011 $\times 10^{-8}$ $m^3 \cdot MPa^{-1}$) for the equipments used. This value was similar to that reported earlier (32), but was much lower than the value given by Miller (24) for his root pressure manometer (0.78 $\mu l \cdot bar^{-1}$). During the measurements, ε_S or $\Delta P_r/\Delta V_S$ also incorporated the elastic extensibility of the root xylem ($\Delta V_x/\Delta P_r$), but it could be shown experimentally that the contribution of the xylem to the overall extensibility was negligible. Introducing a metal rod into the equipment instead of the root did not change ε_S within the limits of the accuracy because ε_x was so large. ΔV_S was evaluated from the movement of the meniscus and the diameter of the capillary.

The hydraulic conductivity of the root, Lp_r (per m^2 of outer surface, A_r) was evaluated from hydrostatic and osmotic relaxation experiments. In the hydrostatic experiments, the root was bathed in nutrient solution. After water flow equilibration ($J_{Vr} = 0$), the position of the meniscus in the capillary was moved forward or backward in order to induce either exosmotic ($J_{Vr} > 0$) or endosmotic ($J_{Vr} < 0$) radial water flows across the root cortex in analogy to experiments with plant cells (*cf.* 34, 35). It is readily shown in Appendix A that the rate constants for endosmotic and exosmotic relaxations should be different and should be of the form:

$$k_{rw} = \frac{\ln(2)}{T^w_{r1/2}} = Lp_r \cdot A_r\left(\frac{\Delta P_r}{\Delta V_S} + f\right), \quad (1)$$

where f is a constant different for exosmotic and endosmotic experiments. The expression ($\Delta P_r/\Delta V_S + f$) is derived from the ratio:

$$\frac{P_{ro} - P_{rA}}{P_{rE} - P_{rA}} = \frac{\varepsilon_S + \frac{V_{So}}{V_x} RT \cdot C_{xo}}{\varepsilon_S} = \frac{\Delta P_r/\Delta V_S + RT \cdot C_{xo}/V_x}{\Delta P_r/\Delta V_S}. \quad (2)$$

Eq. 2 refers to an endosmotic experiment. P_{ro} = original (stationary) root pressure; P_{rA} = initial root pressure produced at $t = 0$; P_{rE} = final (stationary) root pressure.

In the osmotic experiments, relaxation curves were recorded after changing the osmotic pressure of the medium ($RT \cdot C_m$; C_m = osmotic concentration as determined from cryoscopic measurements) while the position of the meniscus was kept constant. An increase in C_m resulted in exosmotic and a decrease in endosmotic relaxation curves. Solutes of both low and high permeability were employed (polyethylene glycol 1000, sucrose, mannitol, ethanol, KNO_3, NaCl). Osmotic Lp_r values could also be evaluated from relaxation curves using Eqs. 1 and 2, although differences are expected particularly in endosmotic experiments, because the osmotic concentration of the xylem sap may increase (see "Results" and Appendix B). The latter point is only relevant when biphasic relaxations are measured.

Measurement of Permeability Coefficients (P_{sr}) and of Reflection Coefficients (σ_{sr}). In the presence of permeating solutes, biphasic relaxations with root pressure minima (P_{rmin}) and maxima (P_{rmax}) were obtained in exosmotic and endosmotic relaxations, respectively. The differences of $P_{ro} - P_{rmin}$ and $P_{ro} - P_{rmax}$ have been used to determine reflection coefficients (see Appendix B). They are given by:

$$\sigma_{sr} = \frac{P_{ro} - P_{rmin}}{RT \cdot C_{ms}} \frac{\varepsilon_x + RT \cdot C_{xo}}{\varepsilon_x} \exp(+k_{rs} \cdot t_{min}) \quad (3)$$

and:

$$\sigma_{sr} = \frac{P_{rmax} - P_{ro}}{RT \cdot C_{xso}} \frac{\Delta P_r/\Delta V_S + RT(C_{xo} + \sigma_{sr} \cdot C_{xso})/V_x}{\Delta P_r/\Delta V_S} \cdot \exp(+k_{rs} \cdot t_{max}). \quad (4)$$

For maize roots, the second fraction on the right side of Eqs. 3 and 4 could be taken as unity to a good approximation, $t_{min(max)}$ could be directly read from the chart record. k_{rs} is the rate constant of the solute phase.

Permeability coefficients of the root for different solutes were evaluated from the second phase of the biphasic relaxations, since:

$$k_{rs} = \frac{P_{sr} \cdot A_r}{V_x}. \quad (5)$$

The volume of the xylem (V_x) was estimated from cross sections (see above) and the outer root surface (A_r) from the root dimensions.

Water Relations Parameters of Root Cortex Cells. Measurements of turgor pressure and of water relations parameters (hydraulic conductivity, Lp; elastic modulus, ε) of individual cortex cells have been made as decribed previously (31–37, 40). Data were obtained for different cell layers, whereby the position of a cell was estimated from the depth of insertion of the tip of the cell pressure probe.

RESULTS

A typical example of hydrostatic relaxations from which the hydraulic conductivity of the root segments was calculated is given in Figure 2. It can be seen that the relaxation processes were rather short ($T^w_{r1/2}$ = 10–20 s). Furthermore, $P_{ro} \neq P_{rE}$ in both the exosmotic and the endosmotic experiments; this is due to concentration effects in the xylem (see Materials and Methods and Appendix A). For the exosmotic experiments, the fact that $P_{rE} > P_{ro}$ is a good indication of the tightness of the seal around the excised root and of the behavior of the root as an osmometer. Osmotic relaxation curves are shown in Figure 3 for different osmotic solutes (NaCl, KNO_3, sucrose, mannitol, and ethanol). It can be seen that for rather permeating solutes such as NaCl or ethanol complete biphasic relaxation curves are obtained. For the other, less permeating substances (KNO_3, mannitol), only the first 'water phase' is shown. The osmotic responses were reversible, *i.e.* upon a reduction of the osmotic concentration the reverse effects occurred (see trace for NaCl in Fig. 3).

In Table I water relations parameters obtained from hydrostatic and osmotic experiments with excised root segments of the main branch of the maize roots are summarized. The data given for the hydraulic conductivity (Lp_r) represent average values for the entire segments. Differences in Lp_r along the root which have been reported for maize (2, 28) and other species (13) have not been resolved in this paper. As indicated by the ranges in Table I, large variations were found in both hydrostatic and osmotic Lp_r values which may be due to differences between roots and also include differences in the variation of Lp_r along the roots. However, the hydrostatic Lp_r was significantly different from the osmotic in both the endosmotic and exosmotic relaxations (*t*-test; $P < 0.001$). The mean values of osmotic Lp_r (1.1 and 1.7 · 10^{-8} $m \cdot s^{-1}$ MPa^{-1}) were by nearly an order of magnitude smaller than the hydrostatic Lp_r (1.2 and 0.9 · 10^{-7} $m \cdot s^{-1}$ MPa^{-1}). This suggests that, depending on the physical nature of the driving force, there is a substantial difference in water transport. The maize root, thus, behaves differently from the barley root for which it has been found that Lp_r (hydrostatic) = Lp_r (osmotic) (32) (see "Discussion").

In Table II we show the differences in osmotic and hydrostatic Lp_r for individual roots in more detail. Only a few examples are

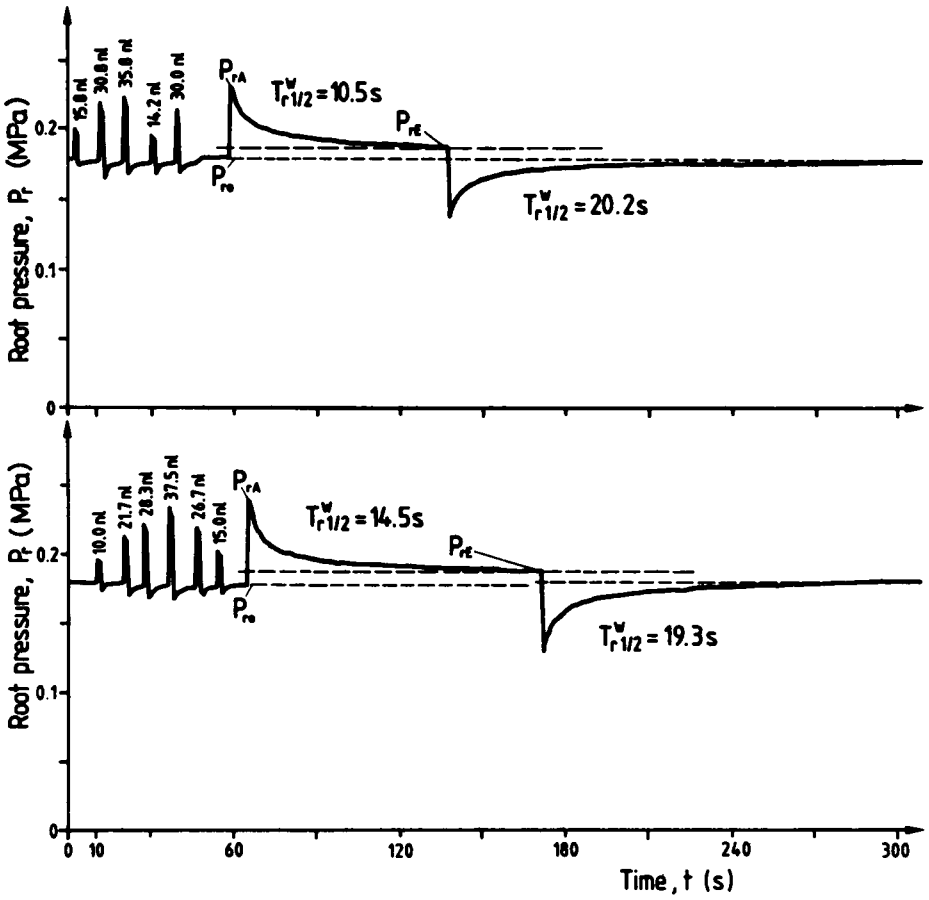

FIG. 2. Root pressure relaxations of an excised maize root measured with the root pressure probe in the 'hydrostatic' type of experiment (Fig. 1). Exosmotic (= direction of water flow from the xylem into the medium) and endosmotic (= direction of water flow from the medium into the xylem) relaxations are shown which are rather rapid ($T^w_{r1/2}$ = 10 to 20 s). From the rate constants (k_{rw}) of the relaxations Lp_r can be calculated according to Eq. 1. Note that the final stationary values (P_{rE}) reached in relaxations are different from the original pressures (P_{ro}) because the root behaves as an osmometer. Peaks on the left side of traces indicate measurements of the extensibility of the measuring system ($\Delta V_S/\Delta P_r$; see "Materials and Methods").

presented which clearly indicate the large differences in the Lp_r obtained by the two types of experiments. We also present the correlation coefficients for the exponential fit by which k^{ex}_{rw} and k^{en}_{rw} values were obtained. The coefficients were close to unity. Only a single phase could be detected in the pressure/time curves within the limits of accuracy.

A polarity in the water movement is also indicated in Tables I and II. In hydrostatic experiments it was found that the hydraulic resistance for the exosmotic water flow was, on average, about 15% smaller (Lp_r^{ex} larger) than the endosmotic. The corresponding ratios of Lp_r^{en}/Lp_r^{ex} were significantly different from unity (*t*-test; $P < 0.001$). The polarity was inversed in the osmotic experiments (*t*-test; $P < 0.01$). To our knowledge, such a polarity of water movement across roots has not yet been reported. It has not been detected for barley using the same technique.

The average stationary root pressure exerted by maize root segments was P_{ro} = 0.12 MPa (Table I). This value is somewhat lower than the values published by Miller (22–24) for the same species but similar to the values obtained for barley (32). Miller (24) has criticized the root pressure probe technique on the grounds that the segments were not supported which could lead to damages which, in turn, result in a lower P_{ro}. This criticism, however, does not seem to be justified because (due to the sensitivity of the technique) the root pressure probe can be used with rather short segments which do not need a support, in comparison with entire root systems, except that they rest on the bottom of the perspex chamber or on a perspex block during the measurement. Further support of the roots did not yield higher P_{ro} values. We think that it is more likely that the differences are due to differences in the varieties used.

In hydrostatic experiments, the half-times of water exchange between root xylem and medium were shorter ($T^w_{r1/2}$ = 2–48 s) for root segments of maize than for barley ($T^w_{r1/2}$ = 170–720 s) because corn roots had a higher hydrostatic Lp_r. On the contrary, the half-times for both species were similar in osmotic experiments. It should be noted that the measured half-times could be different from those of the intact root system. To some extent, the half-times in Table I are also determined by the elastic modulus of the apparatus (ε_S or $\Delta P_r/\Delta V_S$; see Eq. 1) which should be smaller than the elastic modulus of the xylem. Therefore, the $T^w_{r1/2}$ of intact roots is expected to be much shorter. This means that a change of the water potential of the soil should be rapidly transmitted to the root xylem.

Some data for water relations parameters for individual root cortex cells are presented in Table III. These cells showed a behavior comparable to that of other higher plant cells (*cf.* Ref. 35) in that an Lp of some 10^{-7} m·s^{-1} MPa^{-1} was obtained and half-times ranging between 1 and 28 s. The cell turgor ranged between 0.10 and 0.66 MPa with a mean at 0.42 MPa. ε ranged between 1.0 and 18.0 MPa and depended on cell turgor. The fact that the hydrostatic Lp_r was similar to the cell Lp excludes the cell-to-cell path for the water transport across the cortex under hydrostatic conditions and favors an apoplasmic transport within the root cylinder. Otherwise, the hydraulic resistances of several cell layers (membranes) arranged in series would result in a much lower Lp_r. It should be noted that the cell-to-cell path comprises both symplasmic transport via plasmodesmata and transcellular (vacuolar) transport (32).

We have to note that in some cells (7 cells out of 39 investigated) there was a continuous increase in $T^w_{r1/2}$ (decrease in Lp) during repeated measurements on the same cell which resembles earlier findings on cells of the growing pea epicotyl (4) had been discussed in terms of a closing of plasmodesmata during the experiments which, however, could not be proved. S. D. Tyerman (personal communication) recently found a similar behav-

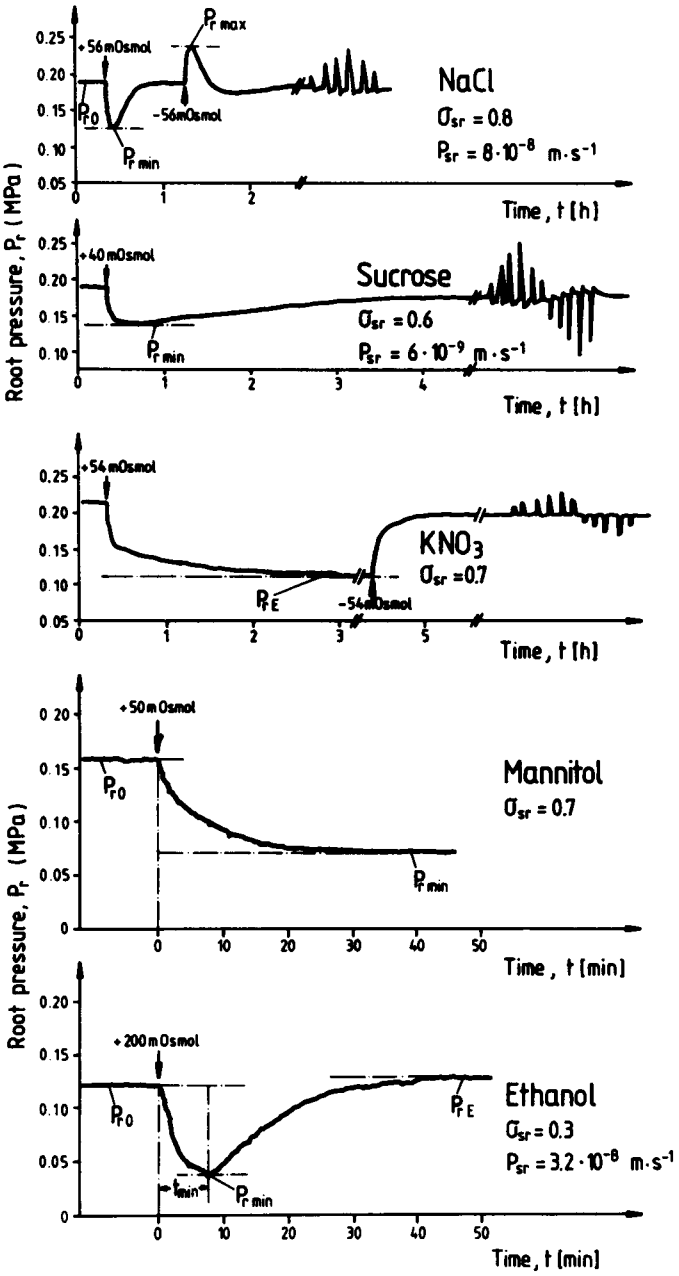

FIG. 3. Responses of root pressure to changes in the osmotic pressure of the medium resulting from different solutes (NaCl, sucrose, KNO_3, mannitol, and ethanol). For the rapidly permeating solutes (NaCl and ethanol) complete biphasic responses are shown (water and solute phase), whereas for the less permeating solutes only the water phases are given. For NaCl it is shown that the pressure responses are reversible, when the solution containing the osmoticum is changed back to the original medium. Half-times of the water phases and of the solute phases yield osmotic Lp_r and permeability coefficient (P_{sr}) of the root. The maximal changes in root pressure ($P_{ro} - P_{min(max)}$) are a measure for the reflection coefficients of the solutes.

ior in root cells of wheat. He also used the cell pressure probe and, by measuring volume relaxations (38), was able to indirectly demonstrate the closing of plasmodesmata from changes of the symplast volume.

The results obtained for reflection and permeability coefficients (Table IV) do show that biphasic pressure relaxation curves can be used to evaluate the coefficients following a theory adapted from that used for algae and higher plant cells (33, 36). Data have been obtained for some electrolytes and nonelectrolytes. They indicate that the uptake of permeating solutes into the root xylem can be directly followed by root pressure measurements. The σ_{sr} values of entire roots were significantly smaller than those of individual cells.

DISCUSSION

The results obtained in this paper show that large differences in the hydraulic properties of maize roots exist depending on whether osmotic or hydrostatic driving forces are involved in water transport. The nature of the driving force also affects the polarity in the water movement across the root. Furthermore, it is demonstrated that the root pressure probe technique is able to measure solute movements across the root besides that of water and to evaluate interactions between flows. However, before these findings are discussed in detail some possible sources of error in the measurements have to be considered.

Two serious arguments against the root pressure probe technique are that excision might change transport properties of roots and that working in the range of positive pressures only is not representative for the situation met in the transpiring plant where negative tensions are exerted within the xylem. Both arguments have to be taken seriously. However, the application of negative pressures (tensions) to the xylem over longer time intervals using the probe causes, at present, enormous technical difficulties. We would like to point out that positive pressures in the xylem also occur naturally during guttation. In any case, the evaluation of hydraulic resistances and of water relations parameters of roots from experiments at a few bar of positive xylem pressure seems to represent a much more 'physiological' condition than pressurizing roots in pressure chambers which may cause substantial changes in ion transport (see discussion in Ref. 27).

The absolute values of the root hydraulic conductivity (Lp_r), found for both osmotic and hydrostatic experiments, are within the range of data given in the literature for maize and other species (Table V). Most of the literature data on Lp_r have been obtained by applying osmotic gradients, and there are only few data which refer to hydrostatic gradients or to a mixture of both. It is interesting that, at least for some species, there is a difference between osmotic and hydrostatic Lp_r similar to that found in this paper when literature values are compared (Table V). This refers to maize, bean, sunflower, and soybean, but not to tomato and barley. The differences of one order of magnitude found between osmotic and hydrostatic Lp_r point to differences in the transport mechanisms. The comparison between cell data (Table III) and root data shows that for hydrostatic gradients the apoplasmic transport component is dominant, whereas for osmotic gradients the contribution of this component should be much smaller. In osmotic experiments, there should be a substantial contribution of the cell-to-cell component (symplasmic plus transcellular transport) to the overall radial water flow.

The result that hydrostatic and osmotic resistances differ largely has been also reported for other tissues using pressure techniques. Steudle and Boyer (31) found differences of 1 to 2 orders of magnitude between hydrostatically and osmotically driven water transport in the growing hypocotyl of soybean, when perfusion and hydration techniques were applied. The radial hydrostatic perfusion of hypocotyl segments yielded Lp_r values which were of the same order or even larger than the cell Lp (apoplasmic transport), whereas hydration of the tissue via the xylem was a slow process which could be only interpreted in terms of a cell-to-cell movement of water. Similarly, the midrib tissue of maize leaves showed quite different transport properties in the absence and in the presence of external hydrostatic gradients (39). In barley roots (32), the situation was different. No significant differences in osmotic and hydrostatic Lp_r were found (Table V). However, changes in the relative importance of the apoplasmic vs. transcellular pathway in roots of the red pine (*Pinus resinosa* Alt.) have been recently reported by Hanson *et*

Table I. *Hydrostatic and Osmotic Hydraulic Conductivity (Lp_r) of Excised Maize Roots as Determined from Rate Constants (Eq. 1) of Root Pressure Relaxations (Figs. 2 and 3)*

Mean values and standard deviations are given as well as ranges for the exosmotic (Lp_r^{ex}) and endosmotic (Lp_r^{en}) Lp_r. The ratios Lp_r^{en}/Lp_r^{ex} have been determined by first averaging Lp_r^{en}/Lp_r^{ex} *from subsequent relaxations of individual roots to eliminate variations in the absolute value of* Lp_r between roots. Numbers in brackets denote the numbers of roots investigated.

	Root Presssure, P_{ro}	Half-Time of Water Exchange, $T_{1/2}^{w}$	Exosmotic Hydraulic Conductivity of Root, $Lp_r^{ex} \times 10^7$	Endosmotic Hydraulic Conductivity of Root, $Lp_r^{en} \times 10^7$	Lp_r^{en}/Lp_r^{ex}
	MPa	*s*	$m \cdot s^{-1} \cdot MPa^{-1}$		
Hydrostatic experiments					
Mean value ± SD	0.12 ± 0.08 (45)		1.15 ± 0.94 (45)	0.94 ± 0.66 (45)	0.87 ± 0.19 (43)
Range	0.01–0.31	2–48	0.13–4.6	0.12–2.8	0.46–1.23
Osmotic experiments					
Mean value ± SD	0.14 ± 0.07 (20)		0.11 ± 0.11 (21)	0.17 ± 0.13 (13)	1.68 ± 0.92 (13)
Range	0.08–0.31	34–690	0.012–0.36	0.010–0.45	0.80–3.56

al. (14). These authors measured the proportion between apoplasmic and total flow across the root using a dye method and found that it could be varied with the pressure applied to the roots. The different results for different species suggest structural differences between different root tissues.

Differences between osmotic and hydrostatic experiments could be explained by the fact that osmotic gradients in the apoplast should not be very effective (as compared with hydrostatic), because of the low reflection coefficient of this structure (σ_r^{apo}). The water flow (J_{Vr}^{apo}) driven by an osmotic gradient ($\Delta\pi$) in the apoplast should be given by:

$$J_{Vr}^{apo} = a_r^{apo} \cdot \sigma_r^{apo} \cdot Lp_r^{apo} \cdot \Delta\pi/d \qquad (6)$$

where a_r^{apo} is the fraction of the mean cross section of the apoplast path, Lp_r^{apo} the hydraulic conductivity of the apoplast, and d the tissue thickness. J_{Vr}^{apo} could be quite high in plant tissues, although a_r^{apo} is only of the order of a few percent, because Lp_r^{apo} is rather large. However, if σ_r^{apo} is close to zero, the contribution of the osmotic flow in the apoplast should become small. In this case, the cell-to-cell path could become important, even though water has to cross quite a number of membrane layers on its passage across the tissue or root.

The differences between the hydraulic resistances of barley and maize roots suggest differences in the hydraulic conductance of the apoplast which may structurally be localized in the endodermis. For young barley roots the Casparian strip seems to be rather tight so that the submicroscopic interfibrillar spaces are interrupted, whereas for the maize root this may not be so, so that a hydrostatic pressure gradient may cause a large flow across the endodermis. It is obvious that, if this picture is correct, the hydrostatic Lp_r of roots like barley or maize should vary with the developmental state of the endodermis. Another reason for the high hydraulic conductivity of maize roots may be found in a large number of secondary initials which have been shown to cause a temporary breach in the Casparian strip (26). These initials could cause an inherent leak in the young main roots used in this paper and could perhaps also explain some of the differences mentioned in the Results section in the absolute values of P_{ro} measured by Miller (who used complete root systems where the percentage of well developed secondary roots was much larger) and in this paper. However, it has to be pointed out that the absolute values of Lp_r have been the same in both studies.

The polarity of water movement found in hydrostatic as well as in osmotic experiments may be due to several reasons. The most important are probably: (a) unstirred layer effects, (b) the presence of a double or multilayer membrane system, and (c) simple mechanical effects which increase Lp_r at increased P_r. In the calculation of Lp_r from hydrostatic experiments possible effects of the dilution or concentration of xylem sap during the relaxations have been accounted for by using an empirical equation (Eq. 1) (see also Eq. 16A). However, there may be sweep away and concentration polarization effects not only within the xylem (which should be influenced by differences in Lp_r along the root; see Appendix A), but also within the complex osmotic barrier of the root which may be comprised not only by the endodermis. If these effects depend on the direction of flow (*e.g.* by a dependence of the thickness of unstirred layers within or at the osmotic barrier on the flow direction; see discussion in Ref. 15, pp. 383–384) the polarity could be accounted for by unstirred layer effects. The second possibility could be that the treatment of the root as a simple two compartment system (as done in this paper) has to be extended. There could be at least two osmotic barriers with different properties (Lp, σ_s, P_s) terminating water and solute flow. For example, if an outer (more permeable) barrier is represented by the endodermis/hypodermis complex or by the entire cortex and an inner (more dense) barrier by the endodermis, a polarity in Lp_r, as found for maize, could be easily accounted for by this asymmetrical structure provided that the reflection coefficient of the outer barrier is smaller than that of the inner one (15, 18, 40). Polarity should increase with increasing J_{Vr} and should vanish for $J_{Vr} \to 0$. In our experiments, changes in J_{Vr} during the relaxations did not affect Lp_r significantly, but the absolute value of J_{Vr} in the experiments could have been too small to produce a measurable non-linear behavior in one direction so that the effects could have been missed. The explanation of a polarity in which $Lp_r^{en} < Lp_r^{ex}$ in terms of a double membrane model as that given above sounds logical, but, in the simple way as it was proposed, is unlikely for roots because it would fail to explain the increase in Lp_r found in plants at high rates of water uptake,

Another reason for the polarity in the hydrostatic Lp_r may be simply mechanical in that the increase of root pressure during exosmotic relaxations causes some distension of root cells or a flow induced deformation of the tissue, thus increasing the cross sectional area for apoplasmic transport. This possibility could also include a reduction of the intercellular air spaces. The latter

Table II. *More Detailed Results for Lp_r and Polarity as in Table I for a Few Excised Maize Roots*

Segment dimensions and the type of experiment are given as well as the correlation coefficient (r) for the exponential fit of the relaxations. The fact that for hydrostatic experiments the fraction $(P_{rA} - P_{ro})/(P_{rA} - P_{rE}) > 1$ demonstrates the osmometer-like behavior of the roots. Lp_r^{en}/Lp_r^{ex} ratios suggest a polarity in the water movement across the root which is different for hydrostatic and osmotic experiments.

Root No.	Segment Length	Mean Diameter	Type of Experiment	*ex/en*	P_{ro}	k_{rw}	$T^w_{\frac{1}{2}h}$	Correlation Coefficient, r	$\frac{P_{rA} - P_{ro}}{P_{rA} - P_{rE}}$	$L_{pr} \times 10^8$	$\bar{L}p_r \times 10^8$	Lp_r^{en}/Lp_r^{ex}
	mm	*mm*			*MPa*	s^{-1}	*s*			$m \cdot s^{-1} \cdot MPa^{-1}$		
1	110	1.14	Hydrostatic	*ex*	0.22	0.0365	19.0	0.93	1.15	4.2	3.1	0.46
				en		0.0149	46.4	0.91	1.02	1.9		
			Osmotic (sucrose)	*ex*		0.00643	107.8	1.00		0.74	1.5	3.1
				en		0.0175	39.7	0.95		2.27		
35	82	0.81	Hydrostatic	*ex*	0.18	0.0444	15.6	0.99	1.18	12.6	10.7	0.67
				en		0.0324	21.4	0.98	1.21	9.0		
				en		0.0219	31.7	0.98	1.09	6.8		
				ex		0.0474	14.6	0.98	1.18	13.5		
				ex		0.0463	15.0	0.99	1.24	12.5		
				en		0.0358	19.3	0.99	1.20	10.0		
			Osmotic (mannitol)	*ex*		0.00186	373	1.00		0.52	0.96	2.8
				en		0.00661	105	0.99		1.90		
				ex		0.0017	408	0.99		0.47		
				en		0.00328	211	0.98		0.94		
37	100	0.93	Hydrostatic	*ex*	0.16	0.0226	30.6	0.99	1.08	6.0	6.1	0.86
				en		0.0254	27.3	0.99	1.15	6.4		
				ex		0.0282	24.6	1.00	1.15	7.1		
				en		0.0199	34.9	0.98	1.19	4.8		
			Osmotic (mannitol)	*ex*		0.00243	286	0.98		0.63	0.78	0.97
				ex		0.00338	205	0.99		0.87		
				en		0.00344	202	1.00		0.85		
42	70	0.86	Hydrostatic	*ex*	0.19	0.0934	7.4	0.98	1.87?	11.2	15.1	0.75
				en		0.0535	13.0	0.92	1.19	10.0		
				ex		0.1140	6.1	0.98	1.22	21.0		
				en		0.0872	8.0	0.96	1.22	16.0		
				ex		0.1080	6.4	0.99	1.19	20.3		
				en		0.0657	10.5	0.96	1.21	12.2		
			Osmotic (sucrose)	*ex*		0.0076	91.3	0.97		1.2	1.4	1.3
				en		0.00855	81.1	0.98		1.6		
44	104	0.79	Hydrostatic	*ex*	0.18	0.0751	9.2	1.00	1.09	22.3	13.8	0.60
				en		0.0710	9.8	0.98	1.34	17.0		
				ex		0.0471	14.7	0.95	1.38	11.0		
				en		0.0238	29.1	0.99	1.56?	4.9		
			Osmotic (NaCl)	*ex*		0.0124	55.9	1.00		3.2	2.9	0.80
				en		0.0117	59.4	0.99		2.6		
45	87	0.93	Hydrostatic	*ex*	0.18	0.0664	10.5	0.99	1.18	15.6	10.7	0.62
				en		0.0343	20.2	0.98	1.24	7.7		
				ex		0.0477	14.5	0.95	1.18	11.2		
				en		0.0360	19.3	0.97	1.18	8.5		
			Osmotic (NaCl)	*ex*		0.0154	45.0	0.98		3.6	4.1	1.2
				en		0.0195	35.5	0.97		4.5		

Table III. *Water Relations Parameters of Individual Root Cortex Cells Determined at Different Depths (12–211 μm) from the root surface*

Since the volumetric elastic modulus (ε) depended on cell turgor, also the turgor pressure ranges for the determination of ε are given. Numbers in parentheses denote the number of cells investigated.

	Turgor Pressure, P	Half-Time of Water Exchange, $T^w_{\frac{1}{2}}$	Elastic Modulus, ε	Range of Turgor for ε	Hydraulic Conductivity of Cell Membrane, $Lp \cdot 10^7$
	MPa	*s*	*MPa*	*MPa*	$m \cdot s^{-1} \cdot MPa^{-1}$
Mean ± SD	0.42 ± 0.12 (39)	8.4 ± 6.0 (39)			2.4 ± 2.0 (39)
Range	0.10–0.66	1.2–28.3	1.3–18.1	0.03–1.00	0.5–8.7

Table IV. *Reflection (σ_{sr}) and Permeability (P_{sr}) Coefficients of Excised End Segments of the Main Branch of Maize Roots*

The coefficients were evaluated from biphasic root pressure relaxations (Fig. 3). Data are given ± SD with the number of roots in parentheses.

Solute	Reflection Coefficient, σ_{sr}	Permeability Coefficient, $P_{sr} \times 10^8$
		$m \cdot s^{-1}$
Ethanol	0.27 ± 0.01(2)	4.7 ± 1.1(2)
Mannitol	0.74 ± 0.20(9)	
Sucrose	0.54 ± 0.22(3)	1.2 ± 0.8(2)
PEG 1000	0.82	
NaCl	0.64 ± 0.28(3)	5.7 ± 3.7(2)
KNO_3	0.67 ± 0.04(2)	

Table V. *Literature Data of Hydraulic Conductivity of Roots (Lp_r) Determined from Either Osmotic or Hydrostatic Type of Experiments for Several Species*

Number in parentheses are references.

Species	Root Hydraulic Conductivity, $Lp_r \cdot 10^8$	
	Osmotic flow	Hydrostatic flow
	$m \cdot s^{-1} \cdot MPa^{-1}$	
Zea mays	5.7(16) 1–12[a] (2, 28) 2.2(25) 4.0(3) 1.2 (this paper)	21(24) (constant flow mode) 10–20 (23) (relaxations) 10 (this paper)
Phaseolus vulgaris	0.56(25)	1–5[b] (29) 8–61 (9, 10)
Helianthus annuus	0.71(25)	2–12[b] (29)
Glycine max	1–14[b] (20)	27(8)
Lycopersicon esculentum	6.1(25)	2–7[b] (29)
Hordeum distichon	0.3–4.3(32) (initial water flow; relaxations)	0.3–4.0(32) (constant flow mode; relaxations)

[a] Lp_r varies along the root. [b] Lp_r increases with increasing J_{vr}.

seems to be rather unlikely, because there is no reason why it should not occur during endosmosis. A filling of intercellular spaces during repeated relaxation experiments could not be observed. Because of the complexity of the system it is, at present, hard to envisage which of the effects mentioned contributes most to the observed polarity. In order to rule out the double membrane hypothesis, the use of root preparations without stele ('sleeves') (11, 12) would be desirable as well as measurements of the Lp of the endodermis using the cell pressure probe. These measurements could help to get quantitative information about the Lp of different barriers in series.

The inverse polarity found in the osmotic experiments is even more difficult to explain in terms of effects like those mentioned above. However, it seems likely that concentration polarization effects in the xylem and diffusion processes within the 'osmotic barrier' (*i.e.* unstirred layer effects) could play a role (see above and Appendix B). Polarization effects could be enhanced if there were regions of high Lp_r along the root. Thus, to decide the origin of the differences in the osmotic Lp_r a more detailed analysis of Lp_r along the root would be desirable.

From the data presented and from the literature data summarized in Table V it seems likely that a dependence of the root hydraulic resistance on the nature of the driving force is also found in other species. The same may be true for the polarity and would be important from a physiological as well as from an ecological point of view. For example, the uptake of water due to tensions in the xylem (hydrostatic gradient) could cause larger water flows across the root than an equivalent change in the osmotic pressure of the soil due to salinity or of the xylem during osmoregulation. Hydration experiments (31) suggest that matric forces should have an effect similar to osmotic gradients. Furthermore, the dependence of water flow on the nature of the driving force and on the flow direction could contribute to the variation of the hydraulic resistance of roots which has been observed in many experiments.

The experiments with permeating solutes show that the root pressure probe could be used to get quantitative data for solute transport in roots. Reflection and permeability coefficients of roots can be evaluated by adapting the theory already used for cells (33, 36) to the root. The reflection coefficients obtained for maize roots were substantially smaller than those of individual cells (see data given in Ref. 33) particularly for solutes which are thought to be 'impermeable' (PEG, mannitol, sucrose, and NaCl). The rather low reflection coefficients may be questioned because they suggest a rather leaky root which may not function properly and should leak nutrients taken up by active processes to a considerable extent. However, our σ_{sr} values are not contradictory in this sense because the P_{sr} values rather than σ_{sr} determine the 'leakiness' of a root. The latter are of an order which does allow a proper function. For example, if P_{sr} is of the order of 10^{-9} to 10^{-10} $m \cdot s^{-1}$ for nutrients as it might be suggested from the experiments shown in Figure 3 (see trace for KNO_3), a maximum leak rate ($J_{sr} = P_{sr}(C_x - C_m)$ can be calculated using a difference in osmotic concentrations between xylem and medium of 60 mOsmol (= 0.15 MPa difference in osmotic pressure). This results in a $J_{sr} = 6$ nmol m^{-2} s^{-1} for $P_{sr} = 10^{-10}$ $m \cdot s^{-1}$, a rate which is still substantially lower than the uptake rates for the main solutes as they have been measured in exudation and tracer experiments (*e.g.* 30–200 $nmol \cdot m^{-2}$ s^{-1} for K^+ and Cl^- for maize; for references see Ref. 1). The finding that for maize quite normal P_{sr} values are correlated with fairly low σ_{sr} values may point to a "correlation" between both parameters different from that observed for cell membranes.

In principle, the finding of rather low reflection coefficients agrees with the rather rare and sometimes contradictory estimates for σ_{sr} reported in the literature. For example, the data of Mees and Weatherley (19) for tomato yield a $\sigma_{sr} = 0.76$ for the nutrients present in the medium, whereas for maize and soybean $\sigma_{sr} = 0.85$ and $\sigma_{sr} = 0.90$ are given, respectively (8, 23). For root segments of maize from which the stele had been removed, also much larger σ_{sr} values are reported (sucrose: 0.98; NaCl: 0.99; urea: 0.85–0.97) (11, 12). These discrepancies are probably due to technical difficulties which include uncertainties resulting from unstirred layers. We agree with Dainty *et al.* (5) that some caution is needed against an easy acceptance of low σ_{sr} values because of unstirred layer effects which reduce the effective osmotic gradient ($RT \cdot C_{ms}$ and $RT \cdot C_{xso}$ in Eqs. 18B and 25B). However, with the root pressure probe these effects can be accounted for, since the solute permeation (diffusion) across the root is also measured and the given values of P_{sr} incorporate unstirred layers. Since the reflection coefficients are corrected for solute flow, the σ_{sr} values given are corrected values, at least to some extent.

In this paper, interactions between water flows across roots and passive solute flows have been dealt with. However, it is obvious that, in principle, the active transport of nutrients could also be followed with the root pressure probe provided that the changes in the osmotic pressure of the xylem caused by active transport are sufficiently large or that the root probe is sufficiently sensitive so that they can be resolved. This type of experiment

should be followed in the future in order to get quantitative data for the relation between nutrition and water uptake. On the other hand, measurements of the hydraulic resistance of different root zones as well as of intact root systems should yield information about the regulation and termination of water uptake. The latter is of particular interest in view of interrelations between stomatal transpiration and root water uptake.

APPENDIX A

CALCULATION OF ROOT HYDRAULIC CONDUCTIVITY (Lp_r) FROM HYDROSTATIC AND OSMOTIC ROOT PRESSURE RELAXATIONS IN THE PRESENCE OF IMPERMEABLE SOLUTES

If the osmotica within the root xylem and in the medium can be taken as impermeable ($\sigma_{sr} = 1$; $P_{sr} = 0$) during the experiments with excised roots, the water flow between xylem and medium (J_{Vr}) will be given by (32)

$$J_{Vr} = -\frac{1}{A_r}\frac{d(V_S + V_x)}{dt} = Lp_r[P_r - RT(C_x - C_m)], \quad (1A)$$

where A_r = root surface area and V_S and V_x are the volume of the measuring system (Fig. 1) and xylem, respectively. P_r is the root pressure and C_x and C_m are the solute concentrations in the xylem and medium, respectively. Due to the experimental arrangement (large volume of external solution), C_m will be constant during an experiment. Eq. 1A assumes a root, or a root segment with a uniform hydraulic conductivity, Lp_r, and xylem concentration, C_x. This assumption may be questionable, because the water permeability may vary in relation to the distance from the root tip. In the case of permeable solutes, the same could be true for the reflection and permeability coefficients of the solutes in the xylem. Differences in P_{sr}, as well as local differences in the activity of the root for the active uptake of nutrients, may lead to gradients in C_x along the root xylem and to a much more complicated relation between water flow and driving forces than that described by Eq. 1A. Eq. 1A averages over different parallel root elements, the transport properties of which are not yet known in detail. This has to be kept in mind, when the system is treated as a simple osmometer with two well-stirred compartments (xylem and medium) separated by a membrane-like osmotic barrier.

It can be shown (see "Materials and Methods") that the xylem vessels are much less extensible than the pressure chamber attached to the root, *i.e.* that the xylem volume, V_x, is practically constant. Therefore, it holds to a good approximation that:

$$\frac{d(V_S + V_x)}{dP_r} \simeq \frac{dV_S}{dP_r} = \frac{V_{So}}{\varepsilon_S} \simeq \frac{\Delta V_S}{\Delta P_r}, \quad (2A)$$

where V_{So} is the reference volume of the measuring system at the stationary, original root pressure, P_{ro}. ε_S is the elastic modulus of the measuring system as defined by Eq. 2A. For small changes in P_r and V_S, $dP_r \simeq P_r - P_{ro}$ and $dV_S \simeq V_S - V_{So}$ and, therefore, Eq. 1A can be written as:

$$\frac{dV_S}{dt} = -Lp_r \cdot A_r \cdot \left[\frac{V_S(t) - V_{So}}{V_{So}}\varepsilon_S + P_{ro} - RT(C_x(t) - C_m)\right]. \quad (3A)$$

This differential equation can be solved, if $C_x(t)$ is known. In an excised root, C_x may be varied by active nutrient uptake, by diffusion of solutes across the cut surface, by osmotic shrinking or swelling of the xylem, and by convective transport of xylem solution across the cut surface during water uptake into the root. Provided that the water transport is much more rapid than the active solute transport this component could be neglected. For impermeable solutes, passive radial diffusion across the root cylinder does not occur. The loss of solutes by diffusion from the cut xylem vessels during the experiments should be very small because the roots are very long (about 100 mm) as compared with the diameter of the vessels. The convective transport of solution during the experiment has to be considered in a different way for exosmotic and endosmotic water flows across the root (see below).

Exosmotic Experiments. In hydrostatic experiments, P_r is changed at $t = 0$ and the position of the meniscus in the capillary is then kept constant. Under exosmotic conditions, $C_x \cdot V_x$ = constant and from Eq. 3A it is obtained:

$$\frac{dV_S}{dt} = -\frac{Lp_r \cdot A_r}{V_{So}} \cdot \varepsilon_S\left(1 + \frac{RT \cdot C_{xo}}{\varepsilon_x}\right)(V_S - V_{So}), \quad (4A)$$

where C_{xo} is the xylem concentration at the original stationary root pressure (P_{ro}) and ε_x is the elastic coefficient of the xylem. In roots, $RT \cdot C_{xo}$ will be usually of the order of a few bar and, thus, much smaller than ε_x. Therefore, in exosmotic experiments the rate constant for the water exchange between the root xylem and surrounding solution, k_{rw}^{ex}, can be approximated by:

$$k_{rw}^{ex} = \frac{Lp_r \cdot A_r}{V_{So}}\varepsilon_S\left(1 + \frac{RT \cdot C_{xo}}{\varepsilon_x}\right) \simeq \frac{Lp_r \cdot A_r \cdot \varepsilon_S}{V_{So}} = Lp_r \cdot A_r \frac{\Delta P_r}{\Delta V_S}. \quad (5A)$$

Considering the boundary conditions ($P_r = P_{rA}$ at $t = 0$ and $P_r = P_{ro}$ at $t \to \infty$), the integration of Eq. 4A yields:

$$\frac{V_S - V_{So}}{V_{So}} = \frac{P_r - P_{ro}}{\varepsilon_S} = \frac{V_{SA} - V_{So}}{V_{So}}\exp(-k_{rw}^{ex} \cdot t) = \frac{P_{rA} - P_{ro}}{\varepsilon_S}\exp(-k_{rw}^{ex} \cdot t), \quad (6A)$$

where V_{SA} is the volume artificially produced at $t = 0$. In the relaxations described by Eq. 6A the final pressure (P_{rE}) reached should, in theory, be identical with P_{ro}. Thus, Eq. 6A differs from the corresponding equation for plant cells (*cf.* Ref 40) in which $P_{rE} > P_{ro}$. This is due to the fact that in the root experiment the pressure chamber is filled with distilled water and the amount of solutes in the xylem ($= C_x \cdot V_x$) is not changing. Concentration changes due to the swelling of the xylem during the relaxation are corrected for by the second term in the brackets in Eq. 5A.

An equation analogous to Eq. 6A may be derived for the osmotic experiment in which an impermeable solute is added to the medium:

$$\frac{V_S - V_{So}}{V_{So}} = \frac{P_r - P_{ro}}{\varepsilon_S} = -\frac{RT \cdot \Delta C_m}{\varepsilon_S\left(1 + \frac{RT \cdot C_{xo}}{\varepsilon_x}\right)}(1 - \exp(-k_{rw}^{ex} \cdot t)) \simeq -\frac{RT \cdot \Delta C_m}{\varepsilon_S}(1 - exp(-k_{rw}^{ex} \cdot t)), \quad (7A)$$

where ΔC_m is the change in the concentration of the impermeable solute in the medium which produces a stationary change in P_r. This change should be close to $RT \cdot \Delta C_m$, if $\varepsilon_x \gg RT \cdot C_{xo}$. Eqs. 5A to 7A show that the rates for the exosmotic root pressure relaxations depend on elastic properties of both the xylem *and* the measuring system. Thus, half-times and rates of water flow measured with the artificial system should, in principle, be different from those of the intact system.

Endosmotic Experiments. As already mentioned, the situation

is different for endosmotic experiments because the uptake of water causes a convection of solution out of the cut end of the root into the measuring system (Fig. 1). The amount of solutes lost is given by $dV_S \cdot C_x$ (32) and it is valid that:

$$-dV_S \cdot C_x = dC_x \cdot V_x, \quad (dV_S > 0) \tag{8A}$$

or:

$$-\frac{V_S - V_{SA}}{V_x} = \frac{C_x - C_{xo}}{C_x} \simeq \frac{C_x - C_{xo}}{C_{xo}}. \tag{9A}$$

Combining Eqs. 9A and 3A yields:

$$\frac{dV_S}{dt} = -k_{rw}^{en}(V_S - V_{So}) - Lp_r \cdot A_r \cdot RT \cdot C_{xo}\frac{V_{So} - V_{SA}}{V_x}, \tag{10A}$$

where k_{rw}^{en} is the rate constant:

$$k_{rw}^{en} = Lp_r \cdot A_r\left(\frac{\varepsilon_S}{V_{So}} + \frac{RT \cdot C_{xo}}{V_x}\right). \tag{11A}$$

It has to be noted that compared with k_{rw}^{ex}, k_{rw}^{en} does not depend on ε_x but on V_x. The second term in the brackets on the right side of Eq. 11A could also become important depending on the absolute value of V_x (*i.e.* on root anatomy). For sufficiently large values of V_x and ε_x, k_{rw}^{ex} and k_{rw}^{en} become equal. This is logical, since the dilution effect in the xylem in the endosmotic experiments as well as the shrinking or swelling effect in the exosmotic experiments will then be small.

Upon integration, Eq. 10A yields:

$$\frac{V_S - V_{SE}}{V_{So}} = \frac{P_r - P_{rE}}{\varepsilon_S} = \frac{P_{rA} - P_{ro}}{\varepsilon_S + V_{So}/V_x\, RT \cdot C_{xo}} \exp(-k_{rw}^{en} \cdot t). \tag{12A}$$

This equation describes the endosmotic $P_r(t)$ curve. Due to dilution $P_{rE} < P_{ro}$, and it is valid that:

$$\frac{P_{ro} - P_{rA}}{P_{rE} - P_{rA}} = \frac{\varepsilon_S + V_{So}/V_x\, RT \cdot C_{xo}}{\varepsilon_S} = \frac{\Delta P_r/\Delta V_S + RT \cdot C_{xo}/V_x}{\Delta P_r/\Delta V_S}. \tag{13A}$$

For the equivalent osmotic experiment the analogous equations are:

$$\frac{V_S - V_{SE}}{V_{So}} = \frac{P_r - P_{rE}}{\varepsilon_S} = \frac{RT \cdot \Delta C_m}{\varepsilon_S + V_{So}/V_x\, RT \cdot C_{xo}} \exp(-k_{rw}^{en} \cdot t) \tag{14A}$$

and:

$$\frac{RT \cdot \Delta C_m}{P_{ro} - P_{rE}} = \frac{\varepsilon_S + V_{So}/V_x\, RT \cdot C_{xo}}{\varepsilon_S}. \tag{15A}$$

$(P_{ro} - P_{rE})$ and $RT \cdot \Delta C_m$ are related to each other by the dilution factor $\varepsilon_S/(\varepsilon_S + V_{So}/V_x \cdot RT \cdot C_{xo})$ which corresponds to the dilution factor of $\varepsilon/(\varepsilon + RT \cdot C)$ in cell experiments.

Practical Equations. Considering Eqs. 6A and 12A there should be, in principle, a difference between the relaxations, because in the exosmotic experiments it is expected that $P_{ro} = P_{rE}$, whereas in the endosmotic $P_{rE} < P_{ro}$. Furthermore, it is expected that $k_{rw}^{en} > k_{rw}^{ex}$. However, it was found in this paper that in hydrostatic experiments $k_{rw}^{en} < k_{rw}^{ex}$ and that in the exosmotic case $P_{rE} > P_{ro}$ (as for cells). The latter would be expected, if processes similar to those considered for the endosmotic case (Eq. 8A) also occur during exosmosis. This may indeed happen, if the root hydraulic conductivity is not uniform. If there are, for example, areas of a larger Lp_r, this could result in local concentration polarizations in the xylem when water flows out which, in turn, could yield a somewhat higher P_{rE} value. In this case, an equation of the same type as Eq. 12A should be used also for the exosmotic experiment, *i.e.*:

$$P_r - P_{rE} = (P_{rA} - P_{rE})\exp(-k_{rw} \cdot t), \tag{16A}$$

where:

$$k_{rw} = Lp_r \cdot A_r\left(\frac{\Delta P_r}{\Delta V_S} + f\right). \tag{17A}$$

f is a constant. $(\Delta P_r/\Delta V_S + f)$ can be evaluated experimentally using Eq. 13A, because P_{ro}, P_{rA}, and P_{rE} are measured and the elasticity of the measuring system, $\Delta P_r/\Delta V_S$, is also determined. If A_r is estimated from the root length and diameter, Lp_r is, thus, obtained for both types of hydrostatic experiments.

In osmotic experiments no ratios of $(P_{rA} - P_{ro})/(P_{rA} - P_{rE})$ can be evaluated for individual relaxations. In this case, the mean values obtained from the parallel hydrostatic experiments have been used in order to correct for the effects described above. It should be noted that the differences between P_{rE} and P_{ro} in the exosmotic relaxations are a good indication for the tightness of the seal between root and pressure probe and for the absence of damages of the root. Severe leakages in the system should result in $P_{rE} < P_{ro}$.

APPENDIX B

CALCULATION OF Lp_r, OF PERMEABILITY COEFFICIENTS (P_s), AND OF REFLECTION COEFFICIENTS (σ_{sr}) FROM OSMOTIC ROOT PRESSURE PROBE EXPERIMENTS: BIPHASIC RELAXATIONS WITH PERMEABLE SOLUTES

The mathematical description of the processes in the presence of a permeable solute resembles that for plant cells (*cf.* Ref. 33). However, there are differences in the root system (two elastic coefficients; xylem system open to measuring system etc.; see Appendix A) which have to be considered. When a permeable solute (subscript 's') is present in the medium, the differential equations describing both, water and solute flows are given by:

$$J_{vr} = -\frac{1}{A_r}\frac{d(V_S + V_x)}{dt} = Lp_r[P_r - RT(C_x - C_m) - \sigma_{sr} \cdot RT(C_{xs} - C_{ms})] \tag{1B}$$

and:

$$J_{sr} = -\frac{1}{A_r}\frac{dn_{sx}}{dt} = P_{sr}(C_{xs} - C_{ms}) + (1 - \sigma_{sr}) \cdot \bar{C}_{rs} \cdot J_{vr}, \tag{2B}$$

where:

n_{sx} = number of moles of 's' in the xylem;
P_{sr} = permeability coefficient of the root to solute 's';
C_{rs} = mean concentration of 's' in the osmotic barrier of the root;
C_{xs} = concentration of 's' in the xylem;
C_{ms} = concentration of 's' in the medium, whereby 's' is added at time $t = 0$ and C_{ms} is kept constant throughout the experiment.

As for the experiments with impermeable solutes (Appendix A), in Eqs. 1B and 2B the root is treated as an osmometer with two compartments. Exosmotic and endosmotic experiments are described by different equations.

Exosmotic Experiments. Using Eq. 2A and remembering that

under exosmotic conditions $C_x \cdot V_x$ = constant, Eq. 1B can be rewritten as:

$$\frac{dV_S}{dt} = -Lp_r \cdot A_r \left[\frac{V_S - V_{So}}{V_{So}} \varepsilon_S \left(1 + \frac{RT \cdot C_{xo}}{\varepsilon_x}\right) - \sigma_{sr} \cdot RT(C_{xs} - C_{ms}) \right]. \quad (3B)$$

Using the dimensionless abbreviations:

$$v_S = \frac{V_S}{V_{So}},$$

$$\tau = \frac{Lp_r \cdot A_r \cdot \varepsilon_S(1 + (RT \cdot C_{xo}/\varepsilon_x))}{V_{So}} t = k_{rw}^{ex} \cdot t, \quad (4B)$$

$$\alpha = \frac{\sigma_{sr} \cdot RT \cdot C_{sm}}{\varepsilon_S(1 + (RT \cdot C_{xo}/\varepsilon_x))}, \text{ and}$$

$$s = \frac{n_{sx}}{V_x \cdot C_{ms}},$$

Eq. 3B yields:

$$\frac{dv_S}{d\tau} = 1 - v_S + \alpha(s - 1). \quad (5B)$$

The equation for the solute flow (Eq. 2B) can be also written in terms of the new variables:

$$\frac{ds}{d\tau} = b(1 - s) + (1 - \sigma_{sr})\frac{\bar{C}_{rs}}{C_{ms}} \frac{V_{So}}{V_x} \frac{dv_S}{d\tau} \quad (6B)$$

with:

$$b \equiv \frac{k_{rs}}{k_{rw}^{ex}}, \text{ and } k_{rs} = \frac{P_{sr} \cdot A_r}{V_x}. \quad (7B)$$

The second term on the right side of Eq. 6B denotes the solvent drag which can be neglected even for rather small values of σ_{sr} (33). Thus, we obtain the two coupled differential equations:

$$\frac{dv_S}{d\tau} = 1 - v_S + \alpha(s - 1) \quad (5B)$$

$$\frac{ds}{d\tau} = b(1 - s). \quad (8B)$$

Considering the boundary condition that for t, $\tau = 0$ the xylem concentration of 's' is C_{xs}, $s = 0$, Eq. 8B is solved by:

$$s = 1 - \exp(-b \cdot \tau). \quad (9B)$$

Combining Eqs. 9B and 5B yields:

$$\frac{dv_S}{d\tau} = 1 - v_S - \alpha \cdot \exp(-b \cdot \tau) \quad (10B)$$

A solution is:

$$v_S = 1 + A[\exp(-\tau) - \exp(-b \cdot \tau)], \quad (11B)$$

where:

$$A = \frac{\alpha}{1 - b}. \quad (12B)$$

Thus, we obtain for the time course of V_S and P_r:

$$\frac{V_S - V_{So}}{V_{So}} = \frac{P_r - P_{ro}}{\varepsilon_S} = \frac{Lp_r \cdot A_r \cdot \sigma_{sr} \cdot RTC_{ms}}{V_{So}(k_{rw}^{ex} - k_{rs})} \cdot [\exp(-k_{rw}^{ex} \cdot t) - \exp(-k_{rs} \cdot t)] \quad (13B)$$

If the extensibility of the xylem can be neglected ($\varepsilon_x \gg RT \cdot C_{xo}$), this can be written as:

$$\frac{V_S - V_{So}}{V_{So}} = \frac{P_r - P_{ro}}{\varepsilon_S} = \frac{Lp_r \cdot \sigma_{sr} \cdot RT \cdot C_{ms}}{Lp_r \cdot \varepsilon_S - V_{So}/V_x P_{sr}} \cdot [\exp(-k_{rw}^{ex} \cdot t) - \exp(-k_{rs} \cdot t)]. \quad (14B)$$

Upon addition of a permeable solute (C_{ms}), P_r first decreases due to a water efflux from the root xylem ('water phase'). The water phase is mainly governed by the first term in the brackets on the right side of Eq. 13B. If this term becomes very small after sufficiently long time periods, the root pressure increases again due to the uptake of solute (term: $\exp(-k_{rs} \cdot t)$). This changes the osmotic gradient across the root and water follows. For the 'solute phase' it is valid that:

$$P_r - P_{ro} = -\sigma_{sr} \cdot RT \cdot C_{ms} \frac{Lp_r \cdot \varepsilon_S}{Lp_r \cdot \varepsilon_S - V_{So}/V_x P_{sr}} \exp(-k_{rs} \cdot t). \quad (15B)$$

k_{rs} and P_{sr} can be obtained from the solute phase. During the water phase, the solute transport influences the rate of water flow depending on the absolute value of b. If the time course of the pressure changes is analyzed in order to evaluate k_{rw}^{ex} (Lp_r), a correction for the solute flow has to be made. Provided that $k_{rw}^{ex} \gg k_{rs}$ it holds that:

$$\frac{P_r - P_{rmin}}{P_{ro} - P_{rmin}} = \exp(+k_{rs} \cdot t_{min}) \cdot [\exp(-k_{rs} \cdot t_{min}) - \exp(-k_{rw}^{ex} \cdot t)] + 1. \quad (16B)$$

(P_{rmin} = minimum root pressure; t_{min} = time to reach the minimum). If k_{rs} and t_{min} are known, k_{rw}^{ex} (Lp_r) can be estimated by an appropriate semilog plot according to Eq. 16B.

At minimum root pressure $dP_r/dt = 0$ and from Eq. 13B it follows that:

$$t_{min} = \frac{1}{k_{rw}^{ex} - k_{rs}} \ln \frac{k_{rw}^{ex}}{k_{rs}}. \quad (17B)$$

This means that t_{min} only depends on k_{rw}^{ex} and k_{rs} and not on the absolute value of σ_{sr} or C_{ms}.

At the minimum, we get from Eq. 13B:

$$\frac{P_{ro} - P_{rmin}}{RT \cdot C_{ms}} = \frac{\varepsilon_x}{\varepsilon_x + RT \cdot C_{xo}} \sigma_{sr} \cdot \exp(-k_{rs} \cdot t_{min}). \quad (18B)$$

Eq. 18B has been used to determine reflection coefficients by measuring ($P_{ro} - P_{rmin}$), t_{min} and k_{rs} for a given change in the osmotic pressure of the permeable solute ($RT \cdot C_{ms}$).

Endosmotic Experiments. In the endosmotic experiments, the roots are equilibrated with permeable solute ($C_{ms} = C_{xso}$) and at $t = 0$, C_{ms} is changed to $C_{ms} = 0$ and is kept there. The resulting biphasic relaxation process with a maximum has to be described. Under the given conditions the equations for the water and solute flow are:

$$J_{Vr} = -\frac{1}{A_r} \frac{d(V_S + V_x)}{dt} = Lp_r[P_r - RT(C_x - C_m) - \sigma_{sr} \cdot RT \cdot C_{xs}] \quad (19B)$$

and:

$$J_{sr} = -\frac{1}{A_r} \frac{dn_{sx}}{dt} = P_{sr} \cdot C_{xs} + (1 - \sigma_{sr})\bar{C}_{rs} \cdot J_{Vr}. \quad (20B)$$

C_{xs} in Eq. 19B may be expressed in terms of V_S analogous to Eq. 9A:

$$-\frac{V_S - V_{So}}{V_x} = \frac{C_{xs} - C_{xso}}{C_{xs}} \simeq \frac{C_{xs} - C_{xso}}{C_{xso}}. \quad (21B)$$

C_{xso} is the xylem concentration at the original stationary pressure P_{ro}. It should be noted that the approximation $C_{xs} \simeq C_{xso}$ is only valid for sufficiently short time intervals following the change of solutions, *i.e.* for intervals during which the amount of '*s*' lost by diffusion across the root cylinder is negligible. This assumption will hold for the entire water phase provided that the rate constant for endosmotic water exchange ($k_{rw}^{en'}$) is substantially larger than k_{rs}. For longer time intervals the assumption does not hold, but for these time periods the water (volume) flow will be governed by solute diffusion (permeability) anyhow.

Using the Eqs. 2A, 9A, and 21B, Eq. 19B can be written as:

$$\frac{dV_S}{dt} = -Lp_r \cdot A_r\left[(V_S - V_{So})\left(\frac{\varepsilon_S}{V_{So}} + \frac{RT}{V_x}(C_{xo} + \sigma_{sr} \cdot C_{xso})\right) - \sigma_{sr} \cdot RT \cdot C_{xso}\right]. \quad (22B)$$

The inspection of Eq. 22B shows that the rate constant for the endosmotic water flow in the presence of a permeable solute ($k_{rw}^{en'}$) differs from k_{rw}^{ex} (Eq. 5A) as well as from k_{rw}^{en} (Eq. 11A). Compared with the latter, the term $\sigma_{sr} \cdot RT \cdot C_{xso}/V_x$ is added which should be constant only during the first period of the experiment (see above):

$$k_{rw}^{en'} = Lp_r \cdot A_r\left[\frac{\varepsilon_S}{V_{So}} + \frac{RT}{V_x}(C_{xo} + \sigma_{sr} \cdot C_{xso})\right]. \quad (23B)$$

The coupled differential Eqs. 19B and 20B can be solved in the same way as for the exosmotic experiment, if the solvent drag can be neglected. The solution is:

$$\frac{V_S - V_{So}}{V_{So}} = \frac{P_r - P_{ro}}{\varepsilon_S} = -\frac{Lp_r \cdot A_r \cdot \sigma_{sr} \cdot RT \cdot C_{xso}}{V_{So}(k_{rw}^{en'} - k_{rs})} \cdot [\exp(-k_{rw}^{en'} \cdot t) - \exp(-k_{rs} \cdot t)]. \quad (24B)$$

This equation has the same structure as Eq. 13B. Provided that the term $\sigma_{sr} \cdot RTC_{xso}/V_x$ in Eq. 23B has some influence on the absolute value of $k_{rw}^{en'}$, *i.e.* if V_x is sufficiently small, we expect that endosmotic curves will become more asymmetric with respect to exosmotic than they could have already been due to the fact that k_{rw}^{ex} is different from k_{rw}^{en}.

As in the exosmotic case, t_{max} will be determined by $k_{rw}^{en'}$ and *krs* according to Eq. 17B. However, t_{max} should be a function of C_{xso}, since $k_{rw}^{en'}$ is a function of C_{xso}.

Reflection coefficients can be evaluated in endosmotic experiments from a relation equivalent to Eq. 18B:

$$\frac{P_{rmax} - P_{ro}}{RT \cdot C_{xso}} = \frac{\varepsilon_S}{\varepsilon_S + V_{So}/V_x\, RT(C_{xo} + \sigma_{sr} \cdot C_{xso})}\, \sigma_{sr} \cdot \exp(k_{rs} \cdot t_{max}). \quad (25B)$$

This relation again emphasizes the differences for exosmotic and endosmotic root experiments. For sufficiently large values of ε_x and V_x, Eqs. 25B and 18B become identical.

In order to evaluate Lp_r from the rate constants of osmotic relaxations, Eqs. 5A and 23B should be used, provided that the influence of the solute flow during the water phase is negligible ($k_{rs} \ll k_{rw}$). In most cases, endosmotic relaxations have been produced right after the water phase of an exosmotic run (*i.e.* without waiting for solute equilibration), so that Eq. 11A instead of Eq. 23B has been used to calculate Lp_r. In the other cases, the expression $[\varepsilon_S/V_{So} + RT(C_{xo} + \sigma_{sr} \cdot C_{xso})/V_x]$ had to be determined. This could be done using Eqs. 18B and 25B which yield:

$$\frac{P_{ro} - P_{rmin}}{P_{rmax} - P_{ro}} = \frac{\varepsilon_S}{\varepsilon_S + V_{So}/V_x\, RT(C_{xo} + \sigma_{sr} \cdot C_{xso})} \cdot \exp(k_{rs}(t_{min} - t_{max})). \quad (26B)$$

Thus, determining P_{ro}, P_{rmin}, P_{rmax}, $\Delta P_r/\Delta V_S$, k_{rs}, t_{max}, and t_{min} yields the expression provided that $\varepsilon_x/(\varepsilon_x + RT \cdot C_{xo})$ can be taken as unity.

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