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Hydraulic propagation of pressure along immature and mature xylem vessels of roots of *Zea mays* measured by pressure-probe techniques

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Abstract. Turgor pressure was measured in cortical cells and in xylem elements of excised roots and roots of intact plants of *Zea mays* L. by means of a cell pressure probe. Turgor of living and hence not fully differentiated late metaxylem (range 0.6–0.8 MPa) was consistently higher than turgor of cortical cells (range 0.4–0.6 MPa) at positions between 40 and 180 mm behind the root tip. Closer to the tip, no turgor difference between the cortex and the stele was measured. The turgor difference indicated that late-metaxylem elements may function as nutrient-storage compartments within the stele. Excised roots were attached to the root pressure probe to precisely manipulate the xylem water potential. Root excision did not affect turgor of cortical cells for at least 8 h. Using the cell pressure probe, the propagation of a hydrostatic pressure change effected by the root pressure probe was recorded in mature and immature xylem elements at various positions along the root. Within seconds, the pressure change propagated along both early and late metaxylems. The half-times of the kinetics, however, were about five times smaller for the early metaxylem, indicating they are likely the major pathway of longitudinal water flow. The hydraulic signal dissipated from the source of the pressure application (cut end of the root) to the tip of the root, presumably because of radial water movement along the root axis. The results demonstrate that the water status of the growth zone and other positions apical to 20 mm is mainly uncoupled from changes of the xylem water potential in the rest of the plant.

Key words: Hydraulic conductivity – Pressure probe (cell and root) – Turgor pressure – Water transport (axial) – Xylem maturation – *Zea* (water transport)

Introduction

On its path through the root, water has to overcome several resistances. The radial pathway, which consists of root tissue between the rhizodermis and the xylem, is conceptually separated from the axial pathway which consists mainly of xylem elements (Passioura 1988). It is the network of hydraulic resistances, rather than the individual components, which determine the sites and amounts of water uptake. This has been theoretically demonstrated by Landsberg and Fowkes (1978) who modeled transport of water through a root system applying the 'cable theory' (Taylor 1963). The theory allows the prediction of water potential gradients along a root from its axial and radial resistances and of the contribution of individual root zones to water uptake or water loss. Profiles of water uptake and water potentials along the xylem have been calculated for an unbranched maize root (Frensch and Steudle 1989) on the basis of the 'cable theory' and measured axial and radial hydraulic resistances using the root pressure probe (RPP) technique (Steudle et al. 1987). In spite of the fact that only protoxylem and early metaxylem (EMX) was mature, Frensch and Steudle (1989) concluded that the axial resistance was not limiting water transport through the root.

As a results of development the hydraulic and osmotic properties of a root change. The finding of living, late metaxylem (LMX) vessels as far as 40 cm behind the root apex of field-grown maize (St. Aubin et al. 1986) indicates that the axial resistance contributes substantially to the total root resistance (radial and axial) and, hence, water uptake may occur mainly in those parts of the root system basal to the maturation of the LMX (McCully and Canny 1988). With maturation of the protoxylem, EMX and LMX, the axial hydraulic resistance declined by five orders of magnitude (Frensch and Steudle 1989; Frensch 1990), and a large change of the xylem water potential along the root was predicted. However, direct measurements of hydrostatic pressures of EMX and LMX and knowledge of the propagation of changes in

Abbreviations and symbols: CPP = cell pressure probe; EMX = early metaxylem; LMX = Late metaxylem; P_c = cell turgor; P_r = root pressure; RPP = root pressure probe; $t_{1/2,c}$ = half-time of water exchange across a single cell; $t_{1/2}$ = half-time of water exchange across multiple cells

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water potential along the root are needed to verify models of water transport through roots.

In this study, we measured turgor of cortical cells and mature and immature xylem elements in maize roots with the cell pressure probe (CPP; Hüsken et al. 1978), to determine effects of xylem maturation on water transport. In combination with the RPP, kinetics of pressure propagation in the xylem were recorded and a profile of xylem water potential along the xylem was established.

Material and methods

Material. After germination for 3 d in the dark, maize (*Zea mays* L., cv. WF 9 × Mo 17) seedlings were grown in a culture solution under a controlled environment (14 h photoperiod; 25° C air temperature). The nutrient solution (Hewitt 1966) contained K^+, Mg^{2+}, Ca^{2+}, and NH_4^+ as major cations, and NO_3^-, $H_2PO_4^-$, and SO_4^{2-} as major anions along with minor nutrients (pH = 6–7). The total concentration was approx. 10 mosmol · kg^{-1}.

Experimental setup. The plant, 3–12 d old, was transferred to the experimental setup with a temperature-controlled root support (Fig. 1). The angle of the root support was adjusted to 70°. The primary root was held to the surface of the support by several magnets placed along the length of the root. The root was covered by flowing nutrient solution identical to that used in growing the plant, circulated by a peristaltic pump.

In experiments on intact plants, the shoot was kept in the dark to reduce transpiration. Turgor pressure was measured in the root cortex at various positions along the root axis using the CPP (Fig. 1). In contrast to the original design (Hüsken et al. 1978), the glass capillary of our CPP was separated from the pressure-controlling unit by a 20-cm-long flexible metal tube (inner diameter 125 µm). The volume increase due to the tube was approx. 10% and did not change the measuring characteristics of the probe noticeably. The arrangement increased the accessibility of the tissue where space was limited and reduced vibration of the capillary caused by the motor-driven control during operation. Capillaries were beveled to obtain an open tip of 3–5 µm. The meniscus between the cell sap and silicone oil of the CPP was observed at magnifications of 64 × to 128 × under a microscope (M24; Wild, Heersburg, Switzerland). To allow precise positioning of the tip inside the tissue, the CPP was mounted on a pneumatic micromanipulator (Narishige, Tokyo, Japan) which moved the glass capillary from cells of the periphery toward cells in the center of the root. Positions of the tip could be determined with an accuracy of 10 µm in the x, y, and z direction using the µm-scale on the manipulator. This was important, since the position of the tip inside the tissue was too deep to be seen.

To manipulate the xylem (root) pressure, the root was cut below the seed and sealed to the RPP (Fig. 1). The RPP functioned as a manometer and recorded the root pressure (P_r) continuously. In contrast to an older version of the RPP (e.g. Steudle et al. 1987), the new version was equipped with a T-junction to apply pressure steps nearly instantly. An external pressurized gas tank was connected to the RPP via a water-filled syringe. With the aid of the external pressure device, the pressure inside the RPP could be rapidly manipulated (half-times of pressure changes <0.1 s). The size of the pressure steps was adjusted with the pressure regulator (Fig. 1) prior to the pressure change. External pressures higher than P_r ($P_{ext} > P_r$) resulted in a water flow out of the syringe into the probe and further into the cut end of the root. External pressures smaller than P_r ($P_{ext} < P_r$) resulted in a volume flow out of the cut end of the root into the probe. Root exudation flow could be stopped when pressure was balanced at $P_{ext} = P_r$. To prevent the propagation of the applied pressure along the cortex rather than through the xylem, the cortex was cut with a scalpel half around the root just below the silicone seal. The treatment did not affect the stationary root pressure.

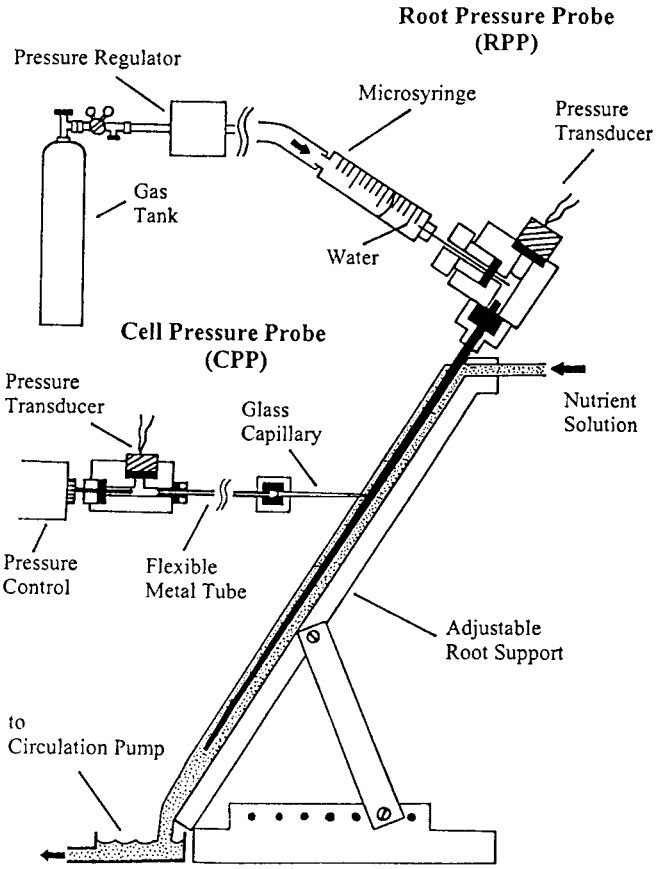

Fig. 1. Experimental arrangement for measuring cell turgor (P_c) while controlling root pressure (P_r) with the root pressure probe (RPP). The primary root was mounted on a temperature-controlled support and was watered by a flowing nutrient solution. With the hypodermic syringe disconnected from the probe, the RPP was closed and functioned as a manometer to record P_r. To apply a hydrostatic pressure change to the cut end of the root, the syringe was connected to the RPP. The pressure inside the RPP was rapidly altered by means of an external pressure device. Along the root axis, stationary as well as transient turgor pressures were measured in the cortex and in the early and late metaxylem using the cell pressure probe (CPP)

Free-hand cross-sections at several positions along the root were made to determine the position of the endodermis, the EMX and the LMX (Fig. 2). Thus, the position of the cell monitored by the CPP could be related to a cell type at the end of the experiment.

Measurement of cellular hydraulic parameters. Measurements of cell turgor (P_c), half-times of water-exchange across single cells ($t_{1/2,c}$), and turgor changes of cells in response to small volume changes ($\Delta P_c/\Delta V_c$) have been described by others (Zimmermann and Steudle 1978). Since the penetration of a cell other than an epidermal cell could not be seen, different cells had to be identified by a different technique. In moving the capillary deeper from one cell to the next, the cell wall and perhaps intercellular space had to be traversed which were at sub-atmospheric or atmospheric pressure. To avoid contamination of the apoplast with oil, the pressure in the CPP was quickly reduced before the tip was moved forward. Crossing the apoplast caused a short bouncing of the meniscus toward the tip of the capillary. The successful impalement of a new cell was indicated by a steady movement of the meniscus toward the base of the capillary. The meniscus was pushed back to the position before the tip was advanced and the depth of insertion determined. The time between two stable turgor readings of two separate cells was less

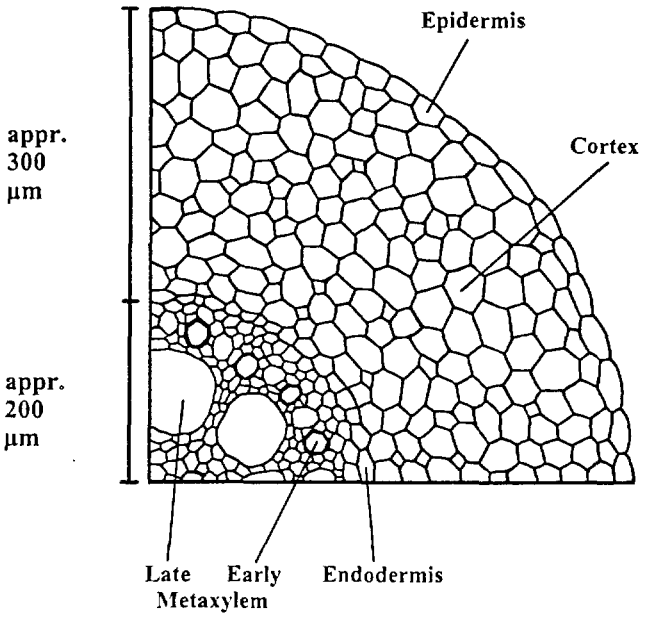

Fig. 2. Drawing of a cross-section prepared from a young maize root (100 mm behind the root tip). Measurements of turgor pressure, half-times of water exchange and cell elasticity were performed on single cells in the cortex, the early and late metaxylem

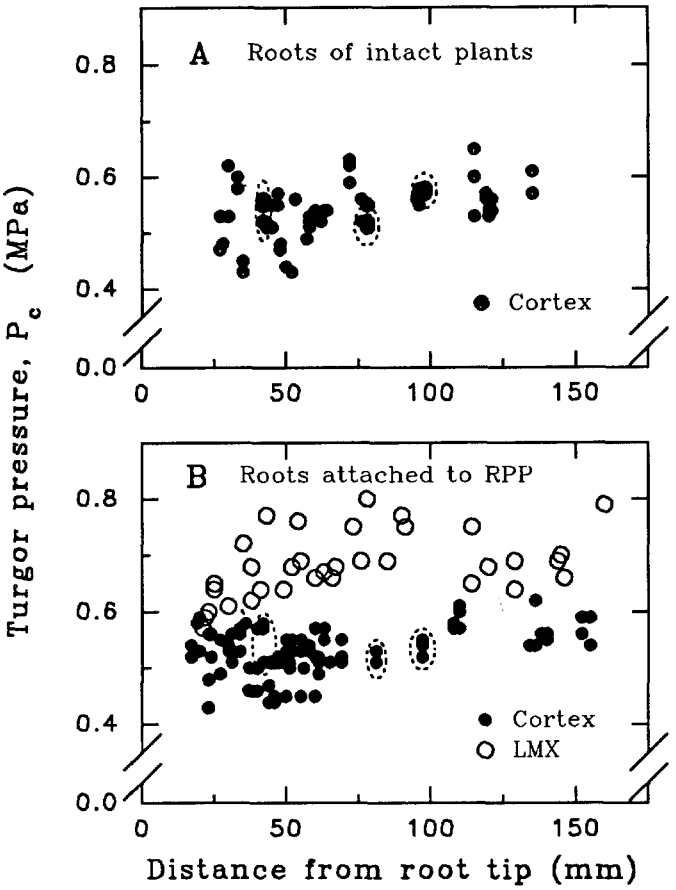

Fig. 3A, B. Spatial distribution of turgor pressures in the cortex (20–100 μm depth) and in the LMX along the maize root. In the intact plant, **A**, the shoot was kept in the dark to minimize transpiration. On excised roots, **B**, the root was attached to the RPP. Nearly stationary conditions (net volume flow, $J_v = 0$) were obtained with the syringe disconnected from the RPP. Data points in **A** and **B** inside dotted lines belong to the same plant before and after mounting to the RPP

than 30 s. The volume of the cell sap entering the capillary and its velocity should depend on the volume and the turgor of the cell being penetrated, provided that the hydraulic resistance of the capillary tip is small. For cortical cells, these parameters were fairly constant. For cells in the stele, volume changes in the capillary were either comparable to those of the cortex or considerably higher. In cases where large volumes entered the capillary, comparison of the depth of insertion and cross-sections of the root indicated that cells of the LMX had been punctured. At the appropriate depth, the LMX was almost always successfully penetrated.

The identification of EMX elements, however, was more complicated. Previous measurements have shown that the transition from living to mature EMX was between 20 and 40 mm behind the root tip (Frensch and Steudle 1989). To identify a mature xylem vessel, P_r was kept higher than the pressure in the CPP. Occasionally, when the capillary advanced to an appropriate position inside the tissue, the meniscus suddenly bounced way back into the capillary. These volume changes were several magnitudes larger than volume changes due to penetration of a cortical cell or of an LMX. Subsequent pressure readings were independent of the position of the meniscus, indicating that the volume was extremely large, as would be expected for an open xylem connected to the RPP.

Results

With the shoot in the dark, P_c was measured on intact plants as well as on excised roots attached to the RPP. In intact plants, P_c in the outer part of the cortex (0 to approx. 100 μm) varied between 0.41 and 0.64 MPa (Fig. 3A). The scatter largely resulted from pressure differences among the different plants ($n = 10$); P_c was largely uniform for a single plant as indicated by data points inside dotted lines in Fig. 3A. Within the first 2 h after roots were excised and sealed to the RPP, roots generated a root pressure of 0.15–0.22 MPa. The turgor pressure in the cortex was largely unaffected by this process and remained relatively constant (Fig. 3B; $n = 13$ plants). Data points enclosed by dotted lines in Figs. 3A and 3B refer to the same plant before and after excision. After roots were mounted to the RPP, no significant decline of turgor could be observed for 8 h (Fig. 4). However, a turgor loss in the cortex of approx. 50% was measured after 24 h. Experiments in this report were conducted within the initial period of 6 h.

In addition to the measurements of the cortex, P_c was also recorded in the LMX of excised roots (Fig. 3B; open symbols). At positions beyond 40 mm behind the root tip, cells of the LMX showed substantially higher turgor pressures than cells of the cortex. The average pressure difference between the cortex and the LMX was 0.2 MPa. The pressure difference (Fig. 3B) appeared to vanish at positions closer to the root tip (e.g. 25 mm).

The propagation of hydrostatic pressure changes was measured in cells of the cortex and the stele. Figure 5 illustrates a typical recording of turgor measurements. The distance of the measuring site to the root tip was 75 mm and to the cut end of the root, 105 mm. The lower trace (dashed line) indicates P_r which was increased

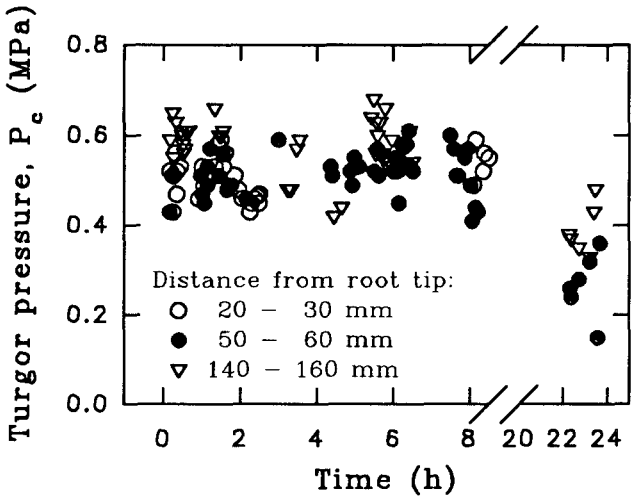

Fig. 4. The effect of root excision on turgor pressure in cortical cells of maize roots. At t = 0 h, an excised root was attached to the RPP. P_c remained rather constant during the initial 8 h of the measurements, regardless of the position along the primary root

and decreased stepwise on demand using the pressure device connected to the RPP. Pressure in a cortical cell, an EMX vessel, and an LMX cell was measured with the CPP (upper trace, solid line) during a period of 680 s. At t = 0 s, the pressure in the RPP was 0 MPa, i.e. the root exuded into the RPP. The capillary of the CPP was introduced into a cortical cell (140 μm inside the root cylinder) and the turgor pressure measured (P_c = 0.57 MPa). From t = 20 to 60 s, two relaxation experiments were performed to determine the half-times of water exchange across a single cell ($t_{1/2,c}$) which is a measure of cellular hydraulic conductivity. A smaller half-time is caused by a larger hydraulic conductivity of the cell. In Fig. 5, $t_{1/2,c}$ was 3.5 s for water flow out of the cell (pressure increase) and 2.2 s for water flow into the cell (pressure decrease). In the time interval between 120 and 480 s, the root pressure was altered with the RPP and the pressure response in the cortical cell recorded. The P_c responded to a change in P_r immediately and $t_{1/2}$ ranged between 8.2 and 16.0 s. The maximum change in P_c relative to the change in applied pressure ($\Delta P_c/\Delta P_r$) was only 0.25 for the cortical cell. During the next 60 s, the capillary was moved toward the center of the root until an element of the EMX was penetrated. The variations in P_c from 485 to 590 s were due to the successive penetration of several intervening cells. The P_c of the EMX was close to 0 MPa at P_r = 0 MPa. As before, P_r was manipulated and the resulting kinetic measured. Before a new steady-state pressure was achieved at t = 595 s, the pressure-time trace exhibited a slight overshoot of the transient pressure. It was due to the re-positioning of the meniscus in the capillary which could not be maintained at a certain position for $t_{1/2} < 0.3$ s. Therefore, half-times smaller than 0.3 s could not be recorded accurately by means of the CPP. Following the pressure step from 0.22 to 0 MPa, a slightly lower pressure (undershoot) than the eventual steady state was applied by the CPP, which again indicated that $t_{1/2}$ was < 0.3 s. When P_r was increased/decreased a second time (between 603 and 608 s), half-times of 0.5 s were measured on the same EMX vessel. For all four pressure jumps, the mean pressure change ± SD of the EMX vessel relative to the applied pressure was 0.50 ± 0.04. By moving the capillary forward by 30 μm at t = 618 s, a cell of the LMX was impaled. The turgor of this cell (P_c) was 0.62 MPa at P_r = 0 MPa. Subsequent pressure-relaxation measurements revealed a $\Delta P_c/\Delta P_r$ of 0.64 ± 0.04, similar to that of the EMX vessel, but substantially higher $t_{1/2}$ values (1.8 and 2.0 s).

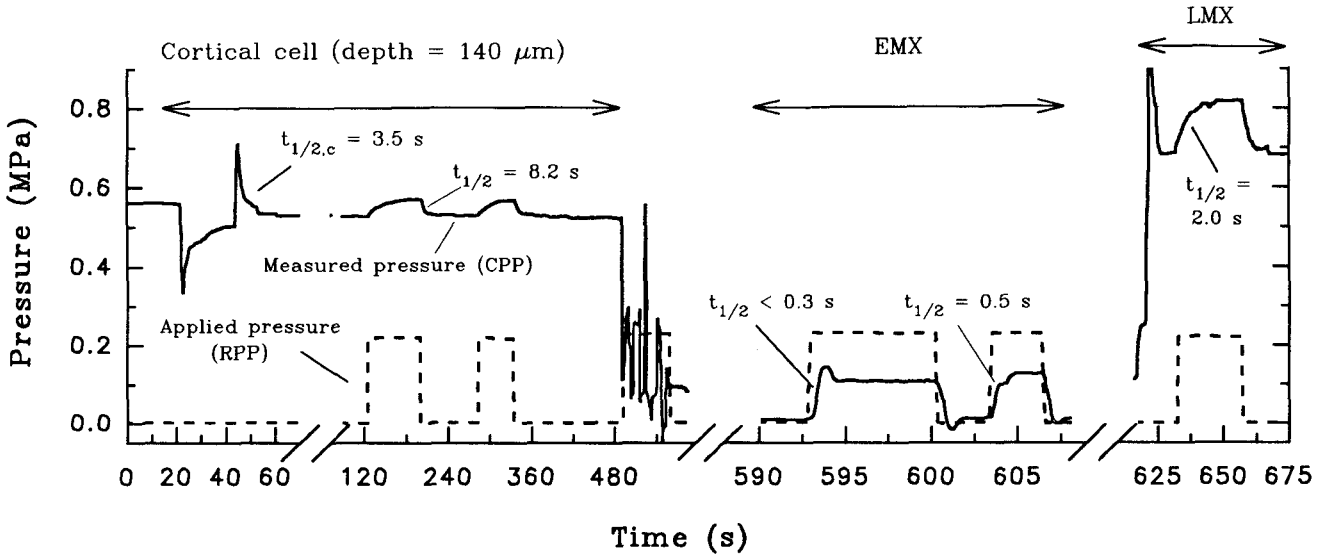

Fig. 5. Time courses of P_c *(solid lines)* in a maize-root cortical cell (t = 0–480 s), in a mature EMX vessel (t = 590–608 s), and in an immature LMX cell (t = 620–675 s) as affected by changes of P_r *(dashed lines)*. To alter xylem water potential, pressure steps were applied to the cut end of an excised root with the aid of the RPP. Turgor responses to changes in P_r were continuously recorded and half-times ($t_{1/2}$) evaluated. Between t = 0 and 60 s, two pressure relaxations were performed using the CPP to obtain cellular half-times ($t_{1/2,c}$) of the cortical cell. Note the different time scales for the different cell types which were chosen to better illustrate the kinetics. Root length = 180 mm, distance between the root tip and the measuring site = 75 mm

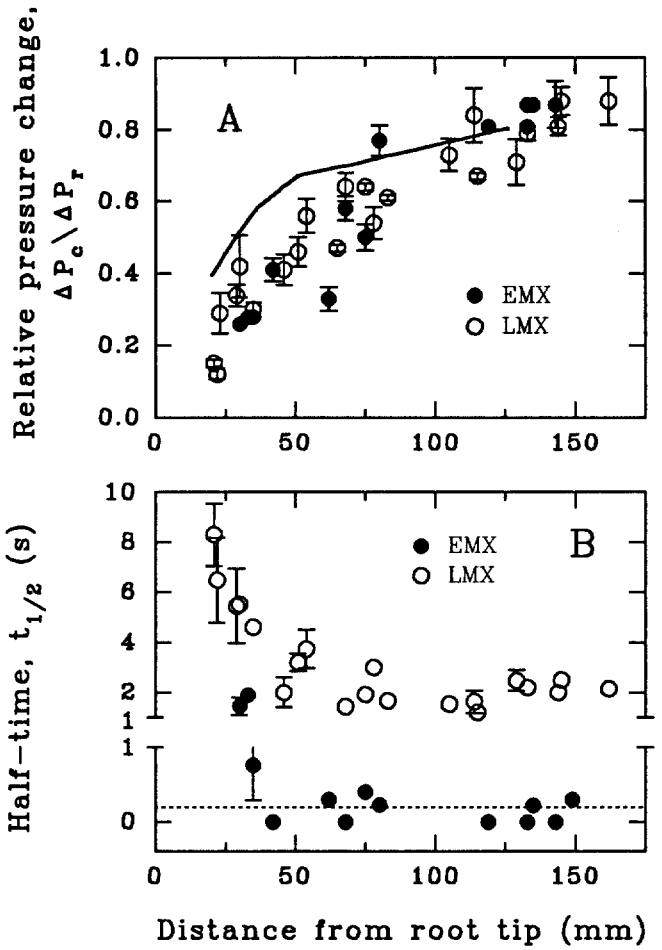

Fig. 6A, B. Propagation of a pressure change along the root axis. **A** Following increases and decreases of pressure steps at the cut end of excised roots, the ratio of measured versus applied pressure change ($\Delta P_c/\Delta P_r$) was determined for elements of the EMX and LMX. The decline of $\Delta P_c/\Delta P_r$ from the base to the tip of the root was mainly due to radial water movement which dissipated the radial driving force. The *solid line* shows a calculation of the pressure decline (adapted from Frensch and Steudle 1989). **B** Half-times ($t_{1/2}$) of the pressure relaxation in the EMX and LMX after a pressure application; $t_{1/2}$ was always higher in the LMX than in the EMX. The *dotted line* indicates the shortest $t_{1/2}$ (0.3 s) detectable by the CPP. Values are means ± SD

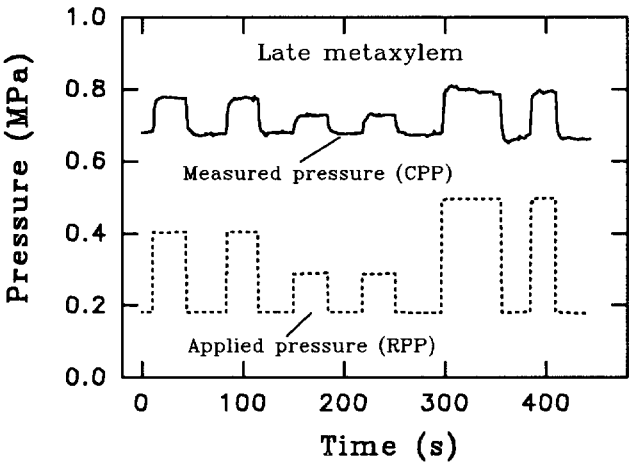

Fig. 7. Response of turgor in the late metaxylem to pressure applications of various magnitudes. Previous to the first pressure step, P_r was 0.18 MPa. Throughout the experiment, the ratio of measured versus applied pressure change ($\Delta P_c/\Delta P_r$) was rather constant (mean ± SD = 0.46 ± 0.04). The mean $t_{1/2}$ ± SD for the pressure increase and decrease of the LMX cell was 3.3 ± 0.3 s. Root length = 182 mm, distance between the root tip and the LMX cell = 51 mm

Table 1. Cellular half-times of water exchange ($t_{1/2,c}$) and changes in cell volume in response to a pressure change ($\Delta P_c/\Delta V_c$) of cells of the EMX and the LMX. For the LMX, the elastic coefficient ($\Sigma_c = V_c \Delta P_c/\Delta V_c$) was estimated assuming an average cell length of 1 mm (St. Aubin et al. 1986) and a radius of 30 μm (Fig. 2). For the EMX, data are presented separately for two intervals. Σ_c was not calculated for the EMX due to uncertainties in estimating V_c of a mature EMX vessel. All values are means ± SD of *n* roots (three to seven repetitions per root)

Xylem type	$t_{1/2,c}$ (S)	$\Delta P_c/\Delta V_c$ (MPa · μl^{-1})	ε_c (MPa)
LMX	1.90 ± 0.33 (*n* = 7)	301 ± 117 (*n* = 7)	0.85
EMX			
20–30 mm	0.41 ± 0.10 (*n* = 3)	–	–
> 30 mm	< 0.3 (*n* = 5)	22 ± 15 (*n* = 5)	–

The results of the pressure-propagation experiments are summarized in Fig. 6. Data points are means ± SD of three to seven replications on nine different roots. In both types of xylem elements, the intensity of the pressure pulse declined toward the root tip with no apparent difference between EMX and LMX (Fig. 6A). Between 170 and 100 mm, the measured pressure response was rather constant and approx. 80% of the applied pressure. The ratio of measured versus applied pressure declined roughly linearly between 80 and 20 mm. At 20 mm behind the tip, only about 15% of the applied pressure step was measured in the xylem. The solid line in Fig. 6A shows a calculation of the pressure decline as predicted from earlier measurements using the RPP (Frensch and Steudle 1989).

The pressure propagation in the EMX was remarkably faster than in the LMX (Fig. 6B). Half-times for the EMX were at or below the limit of detection (0.3 s) for positions between 50 and 150 mm behind the root tip. At more apical positions, mean values of $t_{1/2}$ reached 2 s. Throughout the investigated root lengths, $t_{1/2}$ of the LMX was three to five times higher than $t_{1/2}$ of the EMX.

When pressure changes in the range between 0.05 and 0.32 MPa were effected using the RPP, $\Delta P_c/\Delta P_r$ as well as $t_{1/2}$ for a given cell of the LMX were essentially independent of the magnitude of the applied pressure (Fig. 7).

Half-times of the EMX and LMX were obtained from cell kinetics ($t_{1/2,c}$) as shown for the cortical cell in Fig. 5 and are given in Table 1. Mean values of $t_{1/2,c}$ were similar to values of $t_{1/2}$ determined from pressure/time responses following a pressure application by the RPP. The initial pressure response following a volume change ($\Delta P_c/\Delta V_c$) was by an order of magnitude higher in the LMX than

in the EMX. Theoretically, the difference could be due to different cell volume (V_c) and to different elastic properties of the cell walls. The elastic coefficient ($\varepsilon_c = V_c \Delta P_c / \Delta V_c$) was estimated for the LMX on the basis of measured $\Delta P_c / \Delta V_c$, cell radius = 30 μm (Fig. 2) and cell length = 1 mm (St. Aubin et al. 1986). The average ε_c was in the order of 1 MPa. Smaller values of $\Delta P_c / \Delta V_c$ for the EMX do not necessarily indicate that cells of the EMX were less rigid than vessels of the LMX. Rather, measurements of the ratio $\Delta P_c / \Delta V_c$ indicated that the volume of an EMX vessel exceeded by far the volume of a single LMX cell, since the EMX vessel was in direct contact with the bulk volume of the RPP. Because of the difficulties in correctly determining the effective volume of the EMX, no elastic coefficient was calculated.

Discussion

Measurements using the CPP showed three distinct ranges of hydrostatic pressures across the primary root of young maize seedlings. With no net volume flow across the root, a rather uniform pressure was measured in the cortex, as was reported in other studies for cereal roots (Steudle and Jeschke 1983; Jones et al. 1983; Steudle et al. 1987; Pritchard et al. 1989). In contrast, in the halophytes *Mesembryanthemum crystallinum* (Rygol and Zimmermann 1990) and *Aster tripolium* (Zimmermann et al. 1992) turgor increased from the epidermis toward the center of the root. Zimmermann et al. (1992) found that excision of the root of *A. tripolium* resulted in a dissipation of the radial turgor gradient and argued that the lack of radial turgor gradients, as observed in the present study, were experimental artefacts of excised roots. However, our results indicated no radial turgor gradients in the cortex of roots of intact plants as well as of excised roots. Furthermore, for a period of at least 8 h, turgor in the cortex remained stable.

In the LMX, P_c was substantially higher than in the cortex at positions 40–170 mm behind the root tip. Absolute pressures of the EMX depended on the applied pressure at the cut end of the root: P_c was equal or smaller than the applied pressure. The turgor differences between the two types of xylem elements indicate that the LMX was immature apical to positions of about 200 mm. Living LMX cells were observed up to distances of 400 mm in field-grown maize (St. Aubin et al. 1986), and measurements of the axial hydraulic resistance of hydroponically grown maize indicated maturation of the LMX at positions 200–300 mm behind the tip (Frensch 1990). Therefore, the mature xylem of roots in the present study was presumably restricted to elements of the EMX and protoxylem.

Strictly, the identification of mature and immature xylem does not answer the question on the relative contribution of the different types of xylem to the overall axial volume flow. Because of their large cross-sectional area, the cell-to-cell volume flow along the LMX could still be a significant pathway. Half-times of water exchange along the root axis following a pressure application at the cut end of the root were considerably smaller in the EMX than in the LMX (Fig. 6B). Since half-times of water exchange are a measure of how quickly changes in water potential are propagated across a tissue, a change in water potential propagated much faster in the EMX than in the LMX. During the transition state, much of the pressure changes in the living LMX were presumably caused by radial water movement between EMX and LMX. If water potentials in both EMX and LMX are considered to be lower than the water potential of the medium, water will enter the root and move toward the stele. The arrangement of xylem elements (Fig. 2) dictates that water has to pass the EMX first before it can enter the LMX. In the presence of living LMX, the half-time for axial water flow in the EMX is much smaller than for radial water flow between EMX and LMX. Hence, most of the water will flow longitudinally in the EMX while the LMX will take up only a small amount of water, just enough to balance the radial water potential gradient between the two types of xylem. According to Poiseuille's law, which relates the volume flow at a given pressure difference through a pipe to the fourth power of the pipe's radius, volume flow along the protoxylem should be negligible in the presence of mature EMX, considering diameters of about 20 μm for the EMX and of about 5 μm for the protoxylem.

In solution culture, roots are exposed to uniform conditions of temperature and water and nutrient availability. Their development may therefore differ from roots grown in soil which are exposed to a variable environment. The presence of living LMX in the roots of field-grown maize was closely related to the existence of soil sheaths adhering to the root, while open LMX vessels were mainly present in bare parts of the root which lacked soil sheaths (St. Aubin et al. 1986; Wang et al. 1991). The authors argued that the lack of mature LMX and the subsequent increase of the axial resistance was likely to reduce water uptake substantially in the apical 200–300 mm. However, the impact of the additional axial resistance on water-uptake rates can only be evaluated with the knowledge of both axial and radial hydraulic properties (Landsberg and Fowkes 1978). In young unbranched maize roots, half-times of radial water exchange were in the order of 10–100 s, depending on the nature of the driving force (hydrostatic or osmotic) (Steudle et al. 1987; Steudle and Frensch 1989). At positions proximal to 20 mm, much shorter half-times of a pressure propagation in the EMX ($0.3 < t_{1/2} < 2$ s) were measured in our study. Thus, mature EMX vessels of maize roots still provide a low resistance pathway for longitudinal water flow, at least for an unbranched root axis. A low axial versus radial resistance was also measured in roots of *Vicia faba* (Rowse and Goodman 1981).

The importance of living LMX may not only be discussed in terms of hydraulics. Because of their large volume, LMX cells serve as a storage compartment for nutrients (Anderson and House 1967). This could provide an explanation for the existence of living LMX in sheathed parts of field-grown maize, where water and nutrient uptake presumably was higher than in bare parts of the root (McCully and Canny 1988). Ion transport between living LMX and mature EMX appeared to be

also important in plant adjustment to saline conditions (Frensch et al. 1992). Under almost stationary conditions, i.e. when net volume flow across the root is basically zero, the turgor gradient between the cortex and the LMX strongly indicated higher concentrations of osmotica in the LMX (Fig. 3B). The P_c of the LMX increased at positions 20–50 mm behind the root tip which was indicative of nutrient uptake and accumulation in this part of the root. According to Hylmo's hypothesis (1953), nutrients are passively released from living LMX cells into the transpiration stream at the site of xylem maturation. More recently, a regulated ion transport into and out of the mature xylem has been proposed (De Boer et al. 1983; Johanson and Cheeseman 1983; Clarkson et al. 1984). Regardless of the precise mechanism, the plant might benefit from the nutrient pool during less-favorable external conditions.

We consider that with a low axial resistance, the decline of the pressure response with distance (Fig. 6A) is most likely caused by radial water movement. At a given position along the root, the driving force between the xylem and the medium dissipates due to radial water movement. Consequently, a pressure pulse applied to one end of the xylem also dissipates along the root provided that radial water exchange occurs regularly along the root. About 15% of the applied pressure step was attained in the xylem 25 mm behind the root tip (Fig. 6A). Hence, apical parts, including the growth zone, are essentially isolated from the water status of the rest of the plant. Therefore, the leaf growth zone should be much more exposed to diurnal and seasonal changes of the plant water potential than the root growth zone.

A water potential profile for a shorter root segment (125 mm) was modeled on the basis of measured resistances using the RPP (Frensch and Steudle 1989). It was concluded from the calculations that a young maize plant would benefit little from a mature LMX in terms of water uptake. Basically, measured and calculated profiles of the relative pressure change along the axis (Fig. 6A) agreed reasonably well, assuming that the xylem sap concentration did not change significantly during the short period (few seconds) of pressure response measurements in the present study. The pressure decline from the base to the tip of the root of the calculated profile was slightly smaller than the decline of the measured profile at positions 125–50 mm behind the apex. The deviations are probably caused by small differences in the hydraulic properties of the plant material. Since the axial hydraulic resistance was rather constant 40 to 170 mm behind the apex (Frensch and Steudle 1989; Frensch 1990), the slope of the pressure profile ($\Delta P_c/\Delta P_r$) in Fig. 6A is a measure of the amount of radial water movement. Higher rates of radial water movement 20–100 mm behind the tip compared to more basal positions are indicated by a steeper slope of $\Delta P_c/\Delta P_r$ in this part of the root. Lower rates of radial water movement in basal parts of the root might be related to the development of the endodermis (Peterson et al. 1981; Sanderson 1983).

In conclusion, the mature EMX is a low-resistance pathway in maize roots, indicating that the radial hydraulic properties of the root are rate-limiting in water uptake. Living LMX cells, which persisted all along the investigated root lengths of 160 mm, exhibited high turgor pressures indicative of an internal nutrient pool. The root growth zone is largely isolated from changes in plant water status mainly by two factors: (i) a high axial hydraulic resistance just proximal to the growth zone, and (ii) radial water transport basal to the growth zone.

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