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The integration of whole-root and cellular hydraulic conductivities in cereal roots

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Abstract. The hydraulic conductivities of excised whole root systems of wheat (*Triticum aestivum* L. cv. Atou) and of single excised roots of wheat and maize (*Zea mays* L. cv. Passat) were measured using an osmotically induced back-flow technique. Ninety minutes after excision the values for single excised roots ranged from $1.6 \cdot 10^{-8}$ to $5.5 \cdot 10^{-8}$ $m \cdot s^{-1} \cdot MPa^{-1}$ in wheat and from $0.9 \cdot 10^{-8}$ to $4.8 \cdot 10^{-8}$ $m \cdot s^{-1} \cdot MPa^{-1}$ in maize. The main source of variation was a decrease in the value as root length increased. The hydraulic conductivities of whole root systems, but not of single excised roots, were smaller 15 h after excision. This was not caused by occlusion of the xylem at the cut end of the coleoptile. The hydraulic conductivities of epidermal, cortical and endodermal cells were measured using a pressure probe. Epidermal and cortical cells of both wheat and maize roots gave mean values of $1.2 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$ but in endodermal cells (measured only in wheat) the mean value was $0.5 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$. The cellular hydraulic conductivities were used to calculate the root hydraulic conductivities expected if water flow across the root was via transcellular (vacuole-to-vacuole), apoplasmic or symplasmic pathways. The results indicate that, in freshly excised roots, the bulk of water flow is unlikely to be via the transcellular pathway. This is in contrast to our previous conclusion (H. Jones, A.D. Tomos, R.A. Leigh and R.G. Wyn Jones 1983, Planta 158, 230–236) which was based on results obtained with whole root systems of wheat measured 14–15 h after excision and which probably gave artefactually low values for root hydraulic conductivity. It is now concluded that, near the root tip, water flow could be through a symplasmic pathway in which the only substantial resistances to water flow are provided by the outer epidermal and the inner endodermal plasma membranes. Further from the tip, the measured hydraulic conductivities of the roots are consistent with flow either through the symplasmic or apoplasmic pathways.

Key words: Apoplast – Hydraulic conductivity – Root (hydraulic conductivity) – Symplast – *Triticum* (water conductivity) – Water relations – *Zea* (water conductivity).

Introduction

Water transport across roots is a complex process involving flows through apoplasmic, symplasmic, and transcellular (vacuole-to-vacuole) pathways (for reviews, see Läuchli 1976; Pitman 1977, 1982; Robards and Clarkson 1976). Determining which of these is the preferred route has proved difficult because of the lack of reliable data on the hydraulic conductivities ($L_{p,\,cell}$) of the cell membranes that are interposed into the pathways. With the introduction of the micro-pressure-probe technique (Hüsken et al. 1978) this problem has been largely overcome and it is now possible to measure $L_{p,\,cell}$ and other biophysical parameters that control water transport at the cell level.

Previously we used the pressure probe to measure the water-relation parameters of individual root hair, epidermal, and cortical cells in wheat roots (Jones et al. 1983). The tip of the pressure probe was inserted into the vacuoles of the cells and thus provided values for the $L_{p,\,cell}$ of the plasma membrane and tonoplast in series. These were used to calculate the whole-root hydraulic conduc-

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Symbols: $L_{p,\,cell}$ = cell hydraulic conductivity; $L_{p,\,root}$ = root hydraulic conductivity; $L'_{p,\,root}$ = calculated root hydraulic conductivity; σ = root reflection coefficient

tivity ($L_{p,\,root}$) expected if water flow was via the transcellular pathway. Comparison of this calculated root hydraulic conductivity with that measured using an osmotically induced back-flow technique (Pitman and Wellfare 1978) suggested that the transcellular pathway may be a preferred route for water transport across wheat roots (Jones et al. 1983). A similar study with barley roots came to the same conclusion (Steudle and Jeschke 1983).

Here we report further investigations of the relationships between $L_{p,\,cell}$ and $L_{p,\,root}$. The previous observations have been extended in a number of ways. Firstly, measurements have also been made on maize roots which have a larger diameter than wheat roots and hence a correspondingly greater number of cells interposed into the transcellular pathway. Thus, if this pathway dominates trans-root water flow, $L_{p,\,root}$ should change by an amount dependent on the number of extra cells introduced into the pathway. Secondly, we have overcome technical problems involved in measuring the water-relation parameters of endodermal cells and report values for their $L_{p,\,cell}$. This has allowed us to determine whether the endodermal $L_{p,\,cell}$ dominates $L_{p,\,root}$. Finally, we have studied the effect of root pretreatment on $L_{p,\,root}$ in an attempt to ensure that the previously reported correspondence between the calculated and measured values of $L_{p,\,root}$ was not coincidental. The results have forced a revision of our previous assessment of the importance of the transcellular pathway in water flow across roots. A preliminary report of this work has been published (Jones et al. 1985).

Material and methods

Plant material and chemicals. Seeds of wheat (*Triticum aestivum* L. cv. Atou) and maize (*Zea mays* L. cv. Passat) were surface-sterilized in 1% (v/v) sodium hypochlorite, germinated on filter paper, and grown in half-strength Hoagland's nutrient solution, pH 6.3 (Hoagland and Arnon 1950) as previously described (Jones et al. 1987). Whole root systems (shoot removed but caryopsis still attached) and single roots were excised when seedlings were 4–10 d old and before root branching had occurred. All chemicals were from BDH or Sigma Chemical Company (both of Poole, Dorset, UK).

Measurements with the pressure probe. The $L_{p,\,cell}$ of root hair, epidermal, and cortical cells were measured within 3 cm of the tip of roots of intact seedlings, as previously described (Jones et al. 1983, 1987) but a different technique was used for endodermal cells. For these, the microcapillary of the pressure probe was introduced from the transversely cut end of excised roots. The roots were held in position by inserting their tips into 0.5-mm-diameter capillaries fixed into a drilled Plexiglas block. Endodermal cells were identified as cells at the interface of the stele and the cortex. Measurements were made on endodermal cells located both 1–2 cm and 8–10 cm from the root tip. Epidermal and cortical cells were measured simultaneously to ensure that excision had not affected $L_{p,\,cell}$.

When the measurements on a cell were complete, its dimensions were determined for use in the calculation of $L_{p,\,cell}$. For most cells it was easy to measure their dimensions but in difficult cases, such as endodermal cells, silicone oil was pumped into the cell from the microcapillary of the probe. This made the cell highly refractive and facilitated the measurement of its dimensions. Cell diameters measured in this way were in good agreement with those determined by observation of cells in thin sections. Cell volumes and surface areas were calculated by assuming that epidermal, cortical and endodermal cells were cylindrical and that root hairs were two cylinders.

Measurement of root hydraulic conductivity. An osmotically induced back-flow technique was used (Pitman and Wellfare 1978; Jones et al. 1983). A precision-bore capillary was attached to either a whole root system or a single excised root and the roots were immersed in vigorously aerated half-strength Hoagland's nutrient solution. Xylem fluid was allowed to exude into the capillaries for the times indicated in the text, after which the rate of exudation was measured by following the rise of the meniscus in the capillary. Rates of exudation were linear in all cases. The external solution was then rapidly replaced with nutrient solution which contained 250 $mol \cdot m^{-3}$ D-mannitol. This induced an efflux of water from the surface of the roots which was monitored by measuring the lowering of the meniscus in the capillary. The time course of the efflux was exponential and curves were fitted to the data using a least-squares technique. The initial rate of efflux was calculated from the slope at zero time. The surface area of the roots was determined by measuring root diameters and lengths and, for calculating $L_{p,\,root}$, it was assumed that the whole root surface was conducting. Osmotic pressures of solutions were determined using a Wescor 5100B or 5100C vapour-pressure osmometer (Wescor Inc., Logan, Utah, USA). The hydraulic conductivity of the roots was calculated using the following equation (Pitman and Wellfare 1978):

$$L_{p,\,root} = \frac{J_v + J_{v,\,mann}}{\sigma(\pi_{mann} - \pi_0)} \tag{1}$$

where J_v is the rate of water influx in half-strength Hoagland's nutrient solution, $J_{v,\,mann}$ is the rate of efflux induced by mannitol, π_0 is the osmotic pressure of half-strength Hoagland's nutrient solution, π_{mann} is the osmotic pressure of nutrient solution containing 250 $mol \cdot m^{-3}$ mannitol, and σ is the root reflection coefficient which was assumed to be 1 for all solutes in the system (see *Discussion*).

Measurement of dimensions of cell layers. Sections were cut freehand and were stained with methylene blue. They were examined using a Leitz (Wetzlar, FRG) Ortholux microscope. Cell diameters were measured using an eyepiece graticule. The number of cell layers across the root was also determined from these sections. These data were used to calculate $L_{p,\,root}$ from the measurements of $L_{p,\,cell}$.

Results

$L_{p,\,cell}$. The values obtained for $L_{p,\,cell}$ in different cell types in both wheat and maize roots are shown in Table 1. Visual inspection indicated that the tip of the pressure probe was inserted into the vacuoles of the cells and thus the values of $L_{p,\,cell}$ represent those for the plasma membrane and tonoplast in series. It is assumed that structures such as plasmo-

Table 1. The values of $L_{p, cell}$ for cells in wheat and maize roots. The values of $L_{p, cell}$ were measured with the pressure probe and are for the composite membrane formed by the plasma membrane and tonoplast in series. Values in root hair, epidermal, and cortical cells were measured on cells of roots of intact seedlings but those for endodermal cells on excised roots (see *Materials and methods* for details). n = number of cells measured

Plant	Cell type	$L_{p, cell}$ (10^{-7} m·s^{-1}·MPa^{-1}) Mean ± SD	n
Wheat	Root hair	1.0 ± 0.6	31
	Epidermal	1.2 ± 0.7	42
	Cortical	1.2 ± 1.0	97
	Endodermal [a]	0.5 ± 0.2	25
	Endodermal [b]	0.6 ± 0.1	5
Maize	Epidermal	0.9 ± 0.3	10
	Cortical	1.3 ± 0.7	34

[a] 1–2 cm from root tip
[b] 8–10 cm from root tip

desmata did not contribute to $L_{p, cell}$ and this is supported by the results of Büchner et al. (1981) who found $L_{p, cell}$ to be similar in leaf mesophyll cells and autotrophic suspension-cultured cells of *Chenopodium rubrum* (see also Tomos 1988). The values of $L_{p, cell}$ in Table 1 for root hair, epidermal, and cortical cells of wheat roots are from Jones et al. (1983) and were for cells in roots of intact seedlings. The values for endodermal cells in wheat were obtained by transversely cutting the roots and gaining access to the endodermis via the cut end of the root. To ensure that the cutting had not affected $L_{p, cell}$, simultaneous measurements were made of the $L_{p, cell}$ of cortical and epidermal cells at the cut end. The mean ± SD value for these cells was $1.1 \cdot 10^{-7} \pm 0.4 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1} (n=15) for cells 1–2 cm from the root tip and $1.3 \cdot 10^{-7} \pm 0.6 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1} (n=9) for cells 8–10 cm from the tip. These values are in good agreement with those for these cells in intact roots (Table 1) indicating that excision of the root did not perturb $L_{p, cell}$. It was therefore assumed that the values of $L_{p, cell}$ of the endodermal cells were representative of those in intact roots. The mean $L_{p, cell}$ of the endodermal cells was about $0.5 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1} and thus about half that measured in cortical and epidermal cells of wheat (Table 1). The $L_{p, cell}$ of endodermal cells was unaffected by the distance of the cell from the root tip (Table 1). Measurements on cells of maize roots were restricted to epidermal and cortical cells in roots of intact seedlings and the values were not significantly different from those measured for these cell types in wheat roots (Table 1).

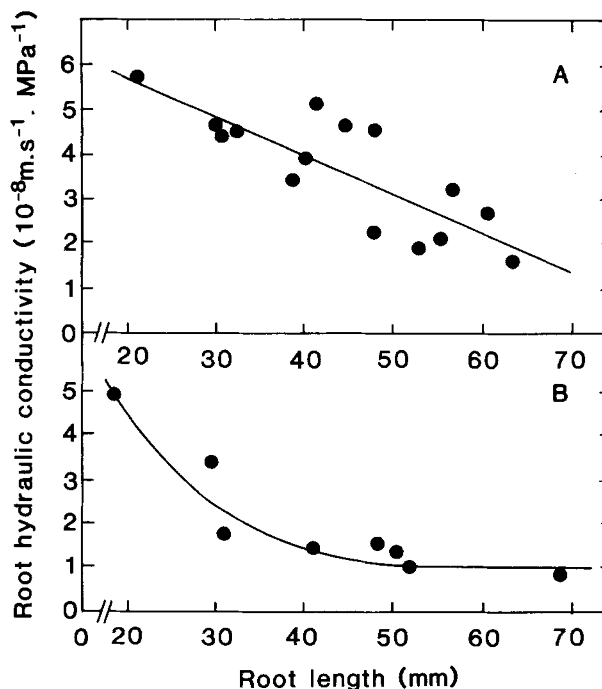

Fig. 1 A, B. Relationship between $L_{p, root}$ and root length in single excised roots of wheat (**A**) or maize (**B**). $L_{p, root}$ was measured using an osmotically induced back-flow technique and measurements were made 90 min after the roots were excised

$L_{p, root}$. The value of $L_{p, root}$ in whole root systems from wheat decreased with time from excision. Ninety minutes after excision, the mean ± SD value was $2.0 \cdot 10^{-8} \pm 1.1 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} (n=7) but after 15 h it was only $0.9 \cdot 10^{-8} \pm 0.2 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} (n=9). This decrease was not due to blockage of the xylem at the cut end of the coleoptile because a value of $0.9 \cdot 10^{-8} \pm 0.2 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} (n=5) was obtained when the coleoptile was re-cut 14 h after excision and measurements made 90 min later. The values of $L_{p, root}$ measured after 15 h were higher than those we reported previously for whole wheat roots, also measured about 15 h after excision (approx $0.5 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1}; Jones et al. 1983). The reason for this is not known with certainty but total root length was longer in the previous study and $L_{p, root}$ decreases with root length (see below). Nonetheless, the data indicate that the $L_{p, root}$ values used in the previous study were not representative of those of recently-excised roots and therefore probably unrepresentative of the values for roots of intact plants. In contrast, there was no time-dependent decline of $L_{p, root}$ when it was measured on single excised roots. The mean ± SD value was $3.7 \cdot 10^{-8} \pm 1.3 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} (n=15) 90 min after excision and $5.1 \cdot 10^{-8} \pm 2.1 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} (n=4) after

15 h. Therefore, further experiments were conducted with single excised primary roots of wheat and maize.

Values for $L_{p,\,root}$ measured on single excised roots varied between $1.6 \cdot 10^{-8}$ and $5.5 \cdot 10^{-8}$ $m \cdot s^{-1} \cdot MPa^{-1}$ in wheat and between $0.9 \cdot 10^{-8}$ and $4.8 \cdot 10^{-8}$ $m \cdot s^{-1} \cdot MPa^{-1}$ in maize. The main source of variation appeared to be the length of root used. In both species the value of $L_{p,\,root}$ declined with root length (Fig. 1). In wheat, the decline was apparently linear up to a root length of 70 mm (Fig. 1 A) but in maize the decline was more exponential and $L_{p,\,root}$ was more or less constant in roots greater than 40 mm in length (Fig. 1 B). The cause of this decline of $L_{p,\,root}$ with root length was not investigated. It is unlikely to be caused by secondary suberization of the endodermis as this only becomes significant at much greater distances from the tip (e.g. Robards et al. 1973).

Calculation of $L_{p,\,root}$ from values of $L_{p,\,cell}$. The value expected for $L_{p,\,root}$ if water flow was via the transcellular (vacuole-to-vacuole), apoplasmic or symplasmic pathways was calculated using the following equation (Kedem and Katchalsky 1963):

$$\frac{1}{L'_{p,\,root}} = \sum_{j=1}^{n} \frac{1}{L_{p,\,j} \cdot A_j} \tag{2}$$

This equation assumes the root consists of a series of concentric rings of membrane where $L_{p,\,j}$ is the hydraulic conductivity of the jth membrane and A_j is its conducting surface area, which diminishes towards the stele. Microscopic examination of roots indicated that the cortex generally consisted of four cell layers in wheat (Fig. 2A) and nine in maize (Fig. 2B). The mean diameters of the cell layers in wheat were (from epidermis inwards to endodermis) 17, 30, 35, 33, 27 and 15 μm. The corresponding values in maize were 21, 24, 26, 37, 36, 48, 43, 49, 34, 27, and 17 μm. The diameter of roots ranged between 450 and 550 μm in wheat and between 900 and 1050 μm in maize. Therefore, root diameters of 500 and 1000 μm were assumed for wheat and maize, respectively.

Transcellular pathway. For this pathway, $L'_{p,\,root}$ was calculated on the assumption that water flowed from vacuole to vacuole across the root, traversing the plasma membrane and tonoplast as it entered and left each cell layer. Thus transport of water from the external medium to the stele of wheat involved six cell layers with 12 concentric membrane elements (each consisting of plasma membrane and tonoplast in series) and in maize, 11 cell layers with 22 membrane elements. For epidermal and cortical cells, $L_{p,\,cell}$ of the combined plasma membrane and tonoplast was assumed to be $1.2 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$, which is the average of the values measured in both wheat and maize (Table 1). For endodermal cells, two different situations were considered. In the first it was assumed that the whole of the measured cell surface area was conducting and hence the $L_{p,\,cell}$ was equal to the measured value of $0.5 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$ (Table 1). In the second, it was assumed that only the tangential membranes were conductive because the radial walls were occluded by the Casparian strip and other impermeable structures so that the effective $L_{p,\,cell}$ was similar to that measured in the other cell types i.e. $1.2 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$.

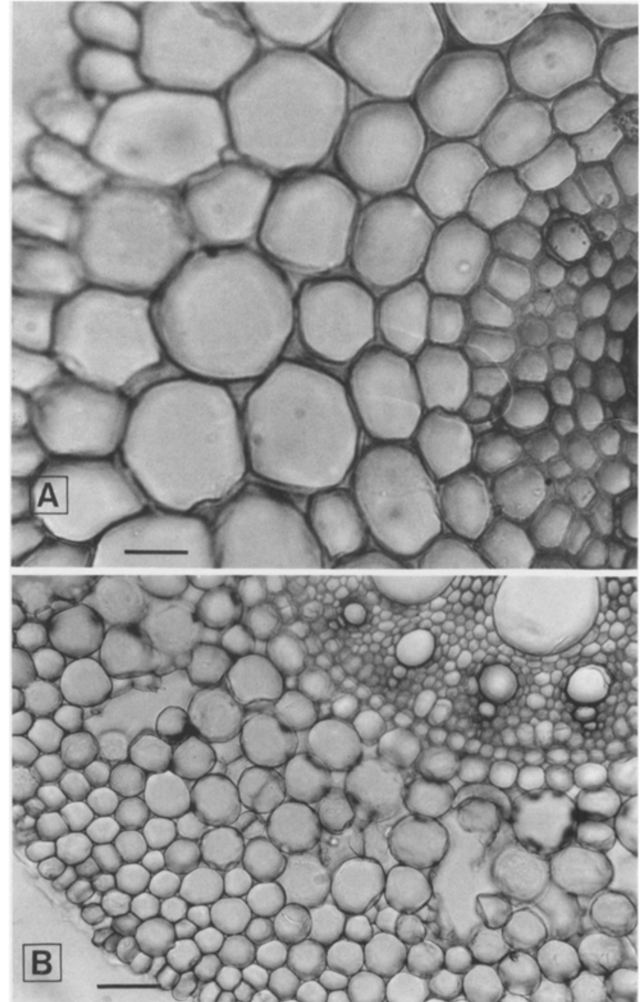

Fig. 2A, B. Light micrographs of hand-cut transverse sections of wheat (**A**) and maize (**B**) roots. **A** ×410, bar = 20 μm; **B** ×140, bar = 60 μm

Using an $L_{p,\,cell}$ for the endodermis of $0.5 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$ yielded a calculated $L'_{p,\,root}$ of

Table 2. The values of $L'_{p,\,root}$ calculated for the transcellular, apoplasmic and symplasmic pathways in roots of wheat and maize. The assumptions underlying the calculations for each of the pathways are given in the text

Plant	Pathway	Assumed value of $L_{p,\,cell}$ (10^{-7} m·s^{-1}·MPa^{-1})		Calculated $L'_{p,\,root}$ (10^{-8} m·s^{-1}·MPa^{-1})
		Epidermal and cortical cells	Endodermis	
Wheat	Transcellular	1.2	1.2	0.61
		1.2	0.5	0.45
	Apoplasmic	–	2.4	4.73
		–	1.0	1.97
	Symplasmic	2.4	2.4	6.43
		2.4	1.0	3.18
Maize	Transcellular	1.2	1.2	0.30
		1.2	0.5	0.24
	Apoplasmic	–	2.4	3.50
		–	1.0	1.46
	Symplasmic	2.4	2.4	5.20
		2.4	1.0	2.48

$0.45 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} for wheat roots and $0.24 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} for maize (Table 2). Increasing the $L_{p,\,cell}$ at the endodermis to $1.2 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1} increased the $L'_{p,\,root}$ to $0.61 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} in wheat and $0.3 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} in maize. In all cases the values were below those for whole root systems of wheat (see above) and for single excised roots of wheat and maize (Fig. 1).

Apoplasmic pathway. The calculation of $L'_{p,\,root}$ for the apoplasmic pathway assumed that water flow across the root was via the apoplast as far as the endodermis but then was forced to flow through the endodermal plasma membrane that faces the cortex, through the cytoplasm, and into the stele by crossing the endodermal plasma membrane that faces the stele. It was assumed that the apoplast had zero resistance and therefore that the only substantial resistances to water flow were at the plasma membrane of the endodermal cells. Further, the resistance to water flow across the plasma membrane was assumed to be half that of the plasma membrane and tonoplast in series and thus its L_p was twice that for the two membranes (see Wendler and Zimmermann 1985). Again, two values for the L_p of this membrane were assumed, $1.0 \cdot 10^{-7}$ and $2.4 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1} (i.e. twice the values assumed above for the plasma membrane and tonoplast of these cells in series). Depending on the value of $L_{p,\,cell}$ assumed, the calculations yielded values of $L'_{p,\,root}$ of $1.97 \cdot 10^{-8}$ or $4.73 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} for wheat roots and $1.46 \cdot 10^{-8}$ or $3.50 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} for maize roots (Table 2).

Symplasmic pathway. For this pathway, water was assumed to enter the symplast across the plasma membrane of the epidermis, flow through the cytoplasm, pass from cell to cell via plasmodesmata of zero resistance, and finally enter the apoplast of the stele by crossing the plasma membrane of the endodermis. The L_p of the epidermal plasma membrane was assumed to be $2.4 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1} and that for the endodermal plasma membrane either $2.4 \cdot 10^{-7}$ or $1.0 \cdot 10^{-7}$ m·s^{-1}·MPa^{-1}. The calculations yielded values of $L'_{p,\,root}$ of $3.18 \cdot 10^{-8}$ or $6.43 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} in wheat and $2.48 \cdot 10^{-8}$ or $5.20 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} in maize (Table 2).

Discussion

The comparisons of root and cellular hydraulic conductivities indicate that, with the possible exception of whole root systems of wheat 15 h after excision (see above and also Jones et al. 1983), the calculated $L'_{p,\,root}$ for the transcellular pathway is less than the $L_{p,\,root}$ measured using an osmotically induced back-flow technique. The implication, therefore, is that some other pathway predominates in freshly excised whole root systems of wheat and in single excised roots of both wheat and maize. The agreement observed previously between the measured $L_{p,\,root}$ of wheat and the calculated value for the transcellular pathway (Jones et al. 1983) appears to have been a consequence of measuring $L_{p,\,root}$ on whole root systems many hours after their excision. Here we have shown that there is a decline in the $L_{p,\,root}$ of whole root systems after their excision. It is unclear whether the $L_{p,\,root}$ declines by chance to values that agree with those calculated for the transcellular pathway or whether the agreement indicates that, some hours after excision, water flow switches to this pathway. We have not investigated the basis of this decline except to show that it is not caused by occlusion of the xylem at the cut end of the coleoptile.

The lack of agreement between the measured values of $L_{p,\,root}$ in freshly excised roots and those calculated for the transcellular pathway are unlikely to be the consequence of errors in the measurement of $L_{p,\,cell}$. The $L_{p,\,root}$ of $1 \cdot 10^{-8}$ to $2 \cdot 10^{-8}$ m·s^{-1}·MPa^{-1} measured in 70-mm-long wheat

and maize roots (Fig. 1) require $L_{p,\,cell}$ values in the range $5 \cdot 10^{-7}$ to $1 \cdot 10^{-6}$ $m \cdot s^{-1} \cdot MPa^{-1}$. These are at the extreme upper end of the range of values measured with the pressure probe and we are unaware of any large, consistent error which could have biased our results to the lower values of $L_{p,\,cell}$ that we obtained. The higher values of $L_{p,\,root}$ measured in short, excised roots require even larger values of $L_{p,\,cell}$ if they are to be explained by the transcellular pathway. In addition, if the transcellular pathway is the preferred route for water flow, then maize roots should have substantially lower $L_{p,\,root}$ values than wheat roots because a greater number of cells are interposed into the pathway (Fig. 2) and thus a greater resistance to water flow is expected. However, the values of $L_{p,\,root}$ measured in maize roots were similar to those of wheat roots (Fig. 1).

Visual observation indicated that the tip of the pressure probe was located in the vacuole and therefore it was assumed that the values of $L_{p,\,cell}$ were those for the plasma membrane and tonoplast in series. However, in electrophysiological studies, the microelectrode often inserts into the cytoplasm and not the vacuole (Findlay and Hope 1976; Bates et al. 1982; Felle and Bertl 1986). If this were also the case with the pressure probe then the measured $L_{p,\,cell}$ would be that for the plasma membrane alone. This would mean that the $L_{p,\,cell}$ for the plasma membrane and tonoplast in series would be lower than the value we have used. Since the calculated value of $L'_{p,\,root}$ decreases proportionately with $L_{p,\,cell}$ (see Equation 2) this would increase the discrepancy between the measured $L_{p,\,root}$ and that expected for the transcellular pathway. Hence the conclusion that the transcellular pathway cannot account for osmotically induced water flow in recently excised roots would not be altered.

For the experimental determination of $L_{p,\,root}$ it was assumed that the root reflection coefficient (σ) was unity for all solutes. Even if the value of σ were less than this, the conclusion that the transcellular pathway does not predominate would not be changed because a lower value of σ would increase the value of $L_{p,\,root}$ (see Equation 1). This would have increased the discrepancy between the measured $L_{p,\,root}$ and that calculated for the transcellular pathway.

Attempting to decide which of the two remaining alternative pathways, the apoplasmic or the symplasmic, predominates in trans-root water flow is complicated by the observation that the measured $L_{p,\,root}$ declines as root length increases (Fig. 1). By comparing the data in Fig. 1 and Table 2, it can be seen that the high values of $L_{p,\,root}$ in 20-mm-long roots are consistent only with the value calculated for a symplasmic pathway with the plasma membrane of both epidermal and endodermal cells having L_p values of $2.4 \cdot 10^{-7}$ $m \cdot s^{-1} \cdot MPa^{-1}$. No other resistances to water flow (e.g. through plasmodesmata) were assumed in the calculation of $L_{p,\,root}$ for this pathway and thus it represents the pathway with the smallest resistance possible if just two membranes with this L_p are involved. In all roots longer than 20 mm the measured values of $L_{p,\,root}$ are consistent with calculated values for either the apoplasmic or the symplasmic pathways. It is thus impossible to decide which, if either, is the preferred pathway for water flow. Further progress will require values for the other resistances to water flow that might be interposed in each of the pathways and which have not been considered in the analysis presented here. In particular, information is needed about the resistances that the cell wall and plasmodesmata provide to water flow through the apoplasmic and symplasmic pathways, respectively.

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