Primary responses of root and leaf elongation to water deficits in the atmosphere and soil solution

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Abstract
Plants experience drought by a limitation of water supply and by enhanced transpiration. Both processes tend to decrease the plant's water potential, but affect growth responses in the root and leaf differently. The evaluation of the underlying mechanisms leads to a discussion of recent studies on biophysical aspects of cell expansion at a cellular, tissue and organ level. Two processes enable roots to compensate rapidly effects of water deficits originating in the medium: (i) adjustment of the minimum pressure in cells required for expansion (yield threshold), and (ii) solute transport within the elongation zone. Limitations of root growth are discussed with respect to hydraulic, mechanical, and solute relations in the root elongation zone. It is argued that the variable nature of both the yield threshold and solute transport challenges the applicability of the Lockhart concept to determine growth-related parameters from steady conditions of turgor and growth. On a whole organ level, the attenuation of xylem pressure along the root is important for the differential response of root and leaf elongation. Experimental evidence is presented for the hydraulic separation of the elongation zones, which is closely related to root development and functioning. The data obtained over the past few years have been used to extend mathematical models of growth and water transport in roots.

Key words: Extension growth, hydraulic conductivity, root development (xylem, endodermis), transport (water and solute), turgor pressure, water stress, xylem pressure, Zea mays.

Introduction
At least during short periods of time, terrestrial plants are exposed to water limiting conditions in almost every natural environment. Cell expansion is among the most sensitive processes in plants affected by drought which is the result of an imbalance in the plant between water uptake and water loss (Hsiao, 1973; Boyer, 1985). Water loss to the atmosphere is largely controlled by stomatal movement. Stomata respond to drought in the atmosphere and in the soil, and much information on the underlying mechanisms has been accumulated (Schulze, 1986; Tardieu and Davies, 1993; Slovik et al., 1995). By contrast, the complexity between root performance and low plant water potentials is much less understood. To maintain uptake of water and nutrients under water limiting conditions, continuous proliferation of roots into new soil layers is important and requires adaptive mechanisms on the cell and tissue level (Tomos et al., 1989; Carpita and Gibeaut, 1993; Cosgrove, 1993).

This review aims to evaluate limitations of root and leaf growth effected by drought in the atmosphere and in the soil. In particular, short-term responses of hydraulic conductivity, cell wall yielding, and solute transport in the root elongation zone are analysed. Furthermore, the significance of root development for the differential response of roots and shoots to drought stress is emphasized and demonstrated. Mechanisms of long-distance volume flow are discussed with respect to new experimental results on pressure propagation in the xylem. Current mathematical models of cell expansion and water uptake are extended on the basis of experimental data.

Differential response of the root and the leaf to water stress: Lockhart's model
For many plants, root growth is more resistant to water stress than shoot growth (Hsiao and Jing, 1987; Kramer and Boyer, 1995). The different responses may be exemplified by a simple experiment. Root and leaf elongation were measured continuously on the same intact plant
which was exposed to various treatments affecting its water status. At steady rates of root and leaf elongation, the seedlings were subjected to an osmotic step change in the medium (Fig. 1A). The osmoticum lowered the water potential of the medium and reduced the water availability instantaneously. Effects of the osmoticum (mannitol) on growth other than a change in water potential were negligible during the short-term period of exposure of 1–2 h (Frensch and Hsiao, 1994). It can be seen in Fig. 1 that root elongation stopped almost immediately upon addition of the osmoticum, but resumed after a few min at a new rate smaller than prior to the treatment. The response of leaf elongation was different in that growth remained stronger inhibited than in the root, at least within the first h of exposure to water stress.

When transpiration was increased by a step change of the humidity inside the gas exchange cuvette a different type of growth response was observed (Fig. 1B). Leaf elongation declined significantly, but root elongation was essentially unaffected. The contrasting behaviour of the two organs indicated that transpiration competed for water with leaf growth rather than with root growth. The fact that growth was less affected in the root than in the leaf may be related to different mechanical and hydraulic properties in these organs (Hsiao and Jing, 1987). An alternative explanation of the differential growth involves the hydraulics of the plant, particularly that of the root. Both issues will be addressed below in detail.

Over the last three decades, the mechanical and hydraulic processes of cell expansion have been analysed using Lockhart’s framework (Lockhart, 1965). Accordingly, the irreversible increase of cell size \( dV/dt \) is associated with a relaxation of the cell wall network, which is driven by a turgor pressure \( P_c \) in excess of a critical threshold \( Y \). A steady cell enlargement is achieved when water uptake just compensates turgor reduction caused by the volume increase of the protoplast. Under these conditions, the governing equation for steady growth of a single cell is:

\[
\frac{dV}{dt} (\frac{1}{mV} + \frac{1}{LpA}) = Y_0 + \pi_c - Y
\]

where \( m \) is the volumetric extensibility coefficient of the

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**Fig. 1.** Simultaneous measurement of root and leaf elongation of a young maize plant. The environment of the shoot was controlled by a gas exchange cuvette; a flowing solution culture covered the primary root clamped to a temperature-controlled root support. Two position transducers (LVDT’s) attached to the first leaf and to the root monitored the plant’s response to changes in water potential effected by (A) osmotic step changes in the medium and (B) increased \( VPD \) (decreased dew point temperature, \( T_{dp} \)). Depending on the nature of the treatment the experiments yielded different types of growth responses in roots and leaves. While a restriction of the water supply affected both organs, although differently during the transition, root growth was largely unaffected upon increasing transpirational demand. Total root length: 150 mm; plant age: 4 d after germination and transfer to growth containers; photosynthetic active radiation at the top of the chamber: approximately 1000 \( \mu \)mol m\(^{-2}\) s\(^{-1}\); air temperature: 24–26 C; nutrient solution similar to a quarter-strength Johnson solution.
wall. $Lp$ is the hydraulic conductivity of the cell. $A$ and $V$ are the surface area and volume of the cell, respectively, $\pi_c$ is the osmotic pressure of the cell sap, and $\Psi_0$ is the water potential of the source. The two terms in brackets represent mechanical and hydraulic 'growth resistances' which limit cell expansion according to their contribution to the overall resistance.

Provided that the mechanical resistance is much larger than the hydraulic, Equation (1) reduces to

$$\frac{dV}{dt} \left( \frac{1}{mV} \right) = P_e - Y$$

(2)

where $(P_e - Y)$ denotes the 'growth-effective turgor'. Equation (2) rather than equation (1) is usually used to quantify cell expansion. When solute transport into the cell is not unlimited, however, the simplified equation can be misleading. Because $\pi_c$ is proportional to the ratio of volume and solute flows ($J_s/J_o$), the criteria for the simplification are not justified solely by showing that $1/(m \times V) \gg 1/(Lp \times A)$ and, thus, $\Psi_0 \approx \Psi_m$ ($\Psi_m$: medium water potential). Rather the relationship between $\pi_c$ and $J_s$ needs further consideration, which is largely ignored in studies relating to cell and tissue growth. It is expected that a separation of solute and water flows would help to elucidate the controversial debate on the significance of hydraulic conductivities for growth.

Conceptually, the differential response of growth in roots and shoots to drought may be summarized in terms of different control loops, linking cell expansion to biophysical and biochemical processes in growing tissues (Bradford and Hsiao, 1982). Turgor pressure ($P_e$) has long been recognized a driving force for cell enlargement, although its meaning for growth control and adjustment to water stress is debated. Doubts about $P_e$ as a limiting factor are based on results from experiments in the field and laboratory (Matsuda and Riazi, 1981; Michelena and Boyer, 1982; Shackel et al., 1987; Hsiao and Jing, 1987; Munns, 1988). However, growth may be sensitive to changes in $P_e$ only where expansion is limited or co-limited by low turgor. This hypothesis was recently investigated by exposing maize plants to changes in water potentials effected in the root medium (osmotic and hydrostatic pressure steps) and in the atmosphere (humidity steps) (French, Hsiao, Rochas-Lara, unpublished results).

The response of the first maize leaf to water deficit was complex and depended on environmental and developmental conditions of the plant (Fig. 2). Highest rates of leaf elongation were obtained when ambient air humidity was high and $\Psi_m$ was close to zero. Any further increase of xylem water potential mediated by small hydrostatic pressure steps in the medium ($0.025$ MPa) failed to increase the leaf elongation rate (Fig. 2, open triangles). Apparently, water was not limiting extension, and sensitivity of growth to changes in $P_e$ was low. With successively less favorable growth conditions (increase of transpiration, $\Psi_m = -0.3$ MPa), leaf elongation benefited from the raise of xylem water potential and additional supply of water. Presumably, the increase of xylem pressure reduced the water potential gradient between the xylem and the surrounding elongating tissue (Nonami and Boyer, 1993). The rather small pressure changes involved illustrate the high sensitivity of leaf elongation to the plant water status when growth was competing with transpiration for water.

A high sensitivity of growth to similar small pressure steps has been previously reported for hypocotyl segments of Vigna (Okamoto et al., 1989). Different from maize, hypocotyls responded transiently to pressure changes which were applied to the solution perfusing the hollow segments. The transient behaviour of hypocotyl growth correlated well with the adjustment of wall rheology. Additional experiments yielded a close correlation between growth adjustment and the acidification of the cell wall solution (Mizuno et al., 1993; Okamoto and Okamoto, 1994). These studies provide evidence for the close coupling of metabolic events and biophysical changes of growth parameters.

**Limitations of Lockhart's model**

Lockhart's model has been proven to be very useful to quantify the growth process of a single cell. None the
less, there are obvious limitations of the model when applied to a growing tissue, which have not yet been incorporated in the theoretical framework. Tissue growth differs from cell growth in that:

(a) growth rates vary along the elongation zones in the plant, corresponding to (i) a spatial heterogeneity in the demand for water and solutes, (ii) variable growth-related parameters with respect to position and time, and (b) water and solutes are supplied by different compartments (e.g. xylem, phloem, soil solution) and transport involves parallel pathways (apoplast and symplast), each with distinct physical and chemical properties.

Measurements at a high spatial and temporal resolution are required to unravel causes and effects within the complex process of tissue growth, and to evaluate tissue response to environmental factors properly.

It is important to recall that equation (2) would predict a linear relationship between $P_e$ and growth rate. Changes of $P_e$ are commonly affected by altering the rate of water uptake by means of changes in $Y_0$, $\pi_n$, and $Lp \times A$. Following perturbations of $P_e$, linearity would justify that $Y$ and $m$ can be determined from steady growth rates and steady turgor pressures. Despite early concerns regarding the linearity (Acevedo et al., 1971; Green et al., 1971) this approach has been extensively used to determine $Y$ and $m$. Alternatively, $Y$ has been determined from turgor relaxation after water uptake into the cell was inhibited (Ortega, 1985; Cosgrove, 1987). However, continuous measurements of $P_e$ during transient responses of growth rates indicate that cell wall parameters are variable and adjust in a matter of min to new environmental conditions (Shackel et al., 1987; Serpe and Matthews, 1992; Frensch and Hsiao, 1994). Without adequate considerations of the variability, previous methods may lead to erroneous values of $Y$ and $m$. Until now, Lockhart's model does not account for the variable nature of any parameter in equation (1). A significant step toward this direction is the modelling of responses of microfibrils in the cell wall to changes in turgor (Passioura and Fry, 1992). Further measurements are required to relate metabolic events with physical restrictions or enhancements of cell expansion.

**The role of solute accumulation for growth**

Water uptake and volume increase of the growing cell constantly dilute the cell sap which would lead to turgor relaxation until growth ceases at $P_e = Y$. Thus, cell expansion is intimately related to solute uptake and/or synthesis. To some extent, equation (1) accounts for this relationship by the parameter $\pi_n$. Introduced as part of the driving force for water flow, $\pi_n$ is also a measure of the solute concentration in the cell. It is evident, however, that equation (1) does not govern the coupling of water and solute flows during cell enlargement. This may be possible by the introduction of a third 'growth resistance' that would couple solute flow to an appropriate force. For example, active solute uptake may be related to the metabolic energy of the cell, whereas passive solute movement into the cell may be driven by a concentration gradient between adjacent cells connected by plasmodesmata.

Depending on the location, the various elongation zones of a plant gain solutes from different compartments. For the root elongation zone, solute accumulation is probably sustained by two compartments, i.e. the soil solution (nutrient salts) and the phloem (carbohydrates, nutrient salts). For above-ground organs, phloem and xylem supply growing cells. To measure rates of solute accumulation in a single cell, consider the following experiment. Turgor is lowered to a level well below $Y$, and cell expansion stops. As long as $P_e < Y$, the irreversible volume increase is zero and changes in $P_e$ would be proportional to changes in water and solute content of that cell. Provided that changes in solute concentration within the protoplasm would be the only process that generates a driving force for water uptake, a change in turgor ($\Delta P_e$) is a measure of the amount of solute accumulated by this cell ($\Delta n_s$), and $\Delta P_e$ is given by (Steudle, 1989, 1992):

$$\Delta P_e = F \left(\frac{\epsilon}{\epsilon + \pi_n} \times \frac{1}{C_c + C_w} \times \left(\frac{RT}{V} \times \frac{\Delta n_s}{C_w + \Delta V_{tissue}}\right)\right).$$

(3)

It can be seen from equation (3) that $\Delta P_e$ corresponds to the increase in $\Delta n_s$ ($\Delta n_s = RT \times \Delta n_s / V$) and $\Delta V_{tissue}$. $\Delta V_{tissue}$ denotes the net volume change of the entire cell (protoplast and cell wall). Changes of $\pi_n$ do not directly translate into $\Delta P_e$. Rather, elastic and plastic deformation of the cell $(F \times \epsilon / (\epsilon + \pi_n)$, $\epsilon$ is the elastic coefficient of a cell) and the storage capacities of the wall $(C_w)$ and the protoplast $(C_c)$ dampen effects of $\Delta n_s$ on $\Delta P_e$. The factor $F$, which is approximately $(1 + \pi_n / m \times \Delta t)^{-1}$ for $\epsilon \gg \pi_n$, accounts for the plastic extension $(m \Delta t)$ of a cell. In contrast to elastic extension $(1 / \epsilon)$, plastic extension is time-dependent; $\Delta t$ denotes the time interval of relative volume increase $(\Delta V / V)$. $F$ approaches 1 for $m \rightarrow 0$ (i.e. in a non-growing cell) and for $\Delta t \rightarrow 0$. If water gain for $\Delta P_e$ is entirely from the apoplasm of the cell, $\Delta V_{tissue} = 0$ and equation (3) becomes

$$\Delta P_e = F \left(\frac{\epsilon}{\epsilon + \pi_n} \times \frac{C_w}{C_c + C_w} \times RT \times \Delta n_s / V \right).$$

(4)

Because of the smaller storage capacity of the wall compared to the protoplast, the ratio $C_w / (C_c + C_w)$ is significantly smaller than unity and changes of $\Delta P_e$ will be small. This relationship may illustrate the situation for shoot growth, when cell expansion strongly competes with transpiration for water. Under these conditions,
omotic adjustment of the growing cell is rather inefficient to maintain \( P_e > Y \).

With sufficient water supply, i.e. water loss in the wall during uptake into the protoplast is immediately replaced by an external water source, \( \Delta V \) equals \( C_e \times RT \times \Delta n_e / V \) (Stemple, 1992). Thus, effects of compartmentation between apoplast and symplast cancel out and equation (3) reduces to

\[
\Delta P_e = F \frac{\epsilon}{\epsilon + \pi_e} \times RT \frac{\Delta n_e}{V}. \tag{5}
\]

Here, \( \Delta n_e \) translates almost entirely into turgor changes provided that \( \epsilon \gg \pi_e \). Equation (5) represents the corresponding turgor change to an increase in solute content of an expanding cell in the root elongation zone when water availability is unlimited. The net deposition rate of solutes into the elongation zone would then be given by:

\[
\frac{\Delta n_e}{\Delta t} = \frac{\Delta P_e}{F} \frac{\epsilon + \pi_e}{\epsilon} \times \frac{V}{RT}. \tag{6}
\]

In the present study, \( \Delta n_e/\Delta t \) was calculated from previous data of \( \Delta P_e/\Delta t \) (Frensch and Hsiao, 1995). The calculations assumed \( F=1 \), because \( \Delta P_e/\Delta t \) was measured at zero root elongation and, hence, \( m \Delta t = 0 \).

A different approach to obtain data on solute accumulation in tissues is to study growth in terms of fluid flow (Silk, 1984). This model yields quantitative information on the magnitude and the spatial distribution of growth along the elongation zone of an organ. Accordingly, net deposition rates of matter for a small root segment are calculated from concentrations of the molecule of interest within this segment and from the local growth rate of this segment. For maize roots, deposition rates of water and several major osmotic compounds have been determined for segments of 0.5 mm length (Sharp et al., 1990). Local deposition rates calculated by this model may be compared with measurements of \( \Delta n_e/\Delta t \) in single cells.

Mechanisms of adaptation to water deficits in roots

It has long been recognized that the expansion rate along the root elongation zone follows a bell-shaped curve. For a maize root, the acceleration and deceleration phases extent over a length of approximately 10 mm (Erickson and Sax, 1956). More recently, elementary growth rates have been combined with turgor measurements. These studies show that turgor is rather uniform throughout the cortex of the elongation zone in spite of large differences in local growth rates in wheat (Pritchard et al., 1990, 1991) and maize (Spollen and Sharp, 1991). Longitudinal gradients in wall rheology are therefore likely the reason for the observed variability in local growth rates (Tomos and Pritchard, 1994). Despite the similarities in both species, a notable difference was observed in these studies when roots were exposed to water stress over medium long periods (hours to days). While maize roots seemed to increase the wall yielding ability, thus maintaining root growth at lower turgor, wheat roots appeared to do just the opposite, i.e. they reduced wall yielding ability. The discrepancy may indicate a fundamental difference between the species during the adjustment to limited water supply.

Further investigations aimed to unravel primary responses in the root elongation zone, including wall rheology and water and solute transport properties, at shorter time intervals (Frensch and Hsiao, 1994, 1995). The results of turgor recordings during steady and dynamic conditions of root growth can be summarized as follows:

(i) Upon exposure of roots to hyperosmotic solutions, \( P_e \) declined rapidly and growth decelerated or stopped almost immediately. However, the inhibition of root growth was compensated partially or completely within min due to both a decline of the yield threshold (\( Y \)) and an osmotic response (\( \Delta P_e \)) that led to a recovery of \( P_e \). A minimum pressure of 0.3 MPa was required for irreversible cell expansion. During the short period of adjustment (1–30 min) the wall extensibility coefficient (\( m \)) remained rather constant.

(ii) The osmotic response of each cell was presumably the result of carbohydrate uptake. Radial solute transport in the elongation zone was sensitive to turgor changes. With successively lower \( P_e \) in the cortex, the rate of solute transport declined drastically.

(iii) Consistent with earlier results on root growth (Sharp et al., 1988), the length of the elongation zone in maize was reduced from originally 10 to approximately 7 mm at \( \phi_m < -0.5 \) MPa. The permanent inhibition of growth in the proximal part of the elongation zone was likely due to the lack of turgor recovery (solute transport). Therefore, \( P_e \) remained smaller than 0.3 MPa, the minimum \( Y \). Towards the apex growth resumed, because radial solute flow continued and exceeded \( Y \) eventually.

(iv) The hydraulic conductivity of the tissue remained high at all levels of \( P_e \). Based on the hydraulic conductivity coefficient of the tissue \( (K = 1.3 \times 10^{-10} \text{ m}^2 \text{ s}^{-1} \text{ MPa}^{-1}) \), gradients of water potential across the cortex were calculated. At maximum expansion rates in the middle of the elongation zone, gradients of only 0.03 MPa would be expected.

On the premise that root elongation stops at \( P_e = Y \), and recalling that \( P_e \) was rather uniform across the cortex, the yield coefficient of the tissue \( (Y_1) \) was determined from the decline of turgor following osmotic step changes in the medium (Fig. 3). The cross-hatched area indicates the approximate pressure gradient in the cortex at which the root elongation rate became zero. Because of the small time interval (few seconds) it took for \( P_e \) to drop
The first phase was due to water loss to the medium and was used to show in Fig. 1. In (C), turgor response was measured in cortical cells pressure (Pc) to step changes of water potential in the medium (V). Accumulation was almost 0.2 MPa Elongation resumed when steady levels at 0.5 MPa. The amount of turgor recovery due to solute addition of the osmoticum, a biphasic pressure response was observed. Indicate periods of continuous measurements during pressure relaxations; the symbols indicate measurements of short intervals. Upon the addition of the osmoticum, a biphasic pressure response was observed. The first phase was due to water loss to the medium and was used to determine the yield threshold of the tissue (Yt) (elongation rate = 0) as well as the hydraulic conductivity coefficient. While elongation was zero, turgor recovered during the second phase and reached a new steady state level at 0.5 MPa. The amount of turgor recovery due to solute accumulation was almost 0.2 MPa. Elongation resumed when Pc reached the yield threshold (Yt), which was already significantly lower than Yt. After the withdrawal of the osmoticum, elongation rate increased to high values. This increase was associated with a large growth-effective turgor (Pc-Yt). The shaded areas indicate possible turgor gradients across the tissue during the determinations of Yt and Y2. The dashed line indicates the possible kinetic of the variable Y. Growth-effective turgor were calculated from the differences (Pc-Yt) and (Pc-Y2). (Adapted from Frensch and Hsiao, 1994.)

from the initial level to Y1, this value probably represents the steady state conditions in the root before the osmoticum was added. While root growth was zero, Pc further declined to a minimum. If the cortical cells in the elongation zone would behave like simple osmometers with semipermeable membranes, as found for mature cells for the short-term duration of the experiment (Frensch and Hsiao, 1994), the pressure would be expected to remain at the low level. However, turgor recovered throughout the cortex, and growth resumed eventually once Pc exceeded the critical pressure. Thus, the yield threshold of the tissue could be determined a second time (Y2) from the kinetics of root elongation and turgor pressure. For the experiment in Fig. 3, the yield threshold declined approximately 0.15 MPa within 15 min, indicating rapid adjustment of the parameter to low Pc. As soon as growth continued, turgor recovery leveled off and reached a new steady state substantially smaller than the original. Yield thresholds (either Y1 or Y2) were by approximately 0.1 MPa lower than the corresponding steady turgor values, which implied that the mechanical resistance (1/(m × V)) did not change significantly during the treatment (equation 2).

After the removal of the osmoticum from the medium, Pc rose and growth rates increased transiently to very high values (Fig. 3B). Evidently, turgor increase generated a large driving force (Pc-Y2) for growth, which presumably declined thereafter due to an increase of Y2.

The variable nature of the yield threshold

A major point of the kinetic study is the observation of the non-linear relationship between root elongation and turgor. Largely, the non-linearity is caused by the variable nature of Y. Within 2–30 min, Y rose to a new value ranging between 0.7 and 0.3 MPa for positions 3 to 10 mm behind the root tip (Frensch and Hsiao, 1995). Apparently, 0.3 MPa was the minimum turgor required for growth. The range represents the 'instantaneous' ability of the root to compensate for turgor changes. Changes of Y are likely to correspond with metabolic processes in the cell wall which trigger both the weakening and hardening of the mechanical network, probably by altering the number of load-bearing tethers between the microfibrils (Passioura and Fry, 1992).

The dynamics of changes in Y are perhaps best demonstrated by continuous recordings of pressure relaxations when water was withheld from entering the tissue (Cosgrove, 1985). The authors detected rapid pressure relaxations of approximately 0.1 MPa throughout the cortex, and growth resumed eventually once Pc exceeded the critical pressure. Thus, the yield threshold of the tissue could be determined a second time (Y2) from the kinetics of root elongation and turgor pressure. For the experiment in Fig. 3, the yield threshold declined approximately 0.15 MPa within 15 min, indicating rapid adjustment of the parameter to low Pc. As soon as growth continued, turgor recovery leveled off and reached a new steady state substantially smaller than the original. Yield thresholds (either Y1 or Y2) were by approximately 0.1 MPa lower than the corresponding steady turgor values, which implied that the mechanical resistance (1/(m × V)) did not change significantly during the treatment (equation 2).

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The dynamics of changes in Y are perhaps best demonstrated by continuous recordings of pressure relaxations when water was withheld from entering the tissue (Cosgrove, 1987, 1993). In these experiments, turgor decayed in a nearly exponential fashion to new steady levels, ranging between 0.1 and 0.3 MPa for various species. Assuming that Y remained constant throughout the pressure relaxation, Cosgrove concluded that the final pressure would indicate the yield threshold of the corresponding tissue. However, in light of the new results on the variability of Y, the basis of interpretation could be quite different. Hence, the pressure relaxation in Cosgrove's experiments may represent the adjustment of Y to the water stress treatment. Accordingly, the final pressure would correspond to the minimum Y. This interpretation is in accordance with measurements on growing soybean stems using the isopiestic psychrometer technique (Boyer et al., 1985). The authors detected rapid pressure relaxations of approximately 0.1 MPa to the
presumed \( Y \), followed by a slower pressure reduction afterwards.

Consistent with the results on leaf growth and results of other studies, \((P_e, Y)\) for roots was small and cell expansion responded to slight changes in \( P_e \) (Matyssek et al., 1988; Okamoto et al., 1989). Compared with the conventional method, i.e. when \( Y \) is calculated from steady state relationships between growth rate and \( P_e \), the direct approach yielded much higher values of \( Y \) and, thus, smaller values of \((P_e-Y)\) (Frensch and Hsiao, 1994). The discrepancy may caution to evaluate \( Y \) and \( m \) applying the linear relationship of the Lockhart equation to experiments where the water status of the root is altered. Earlier conclusions drawn on the assumption that \( Y \) behaves like a constant may be premature.

**Is the determination of \( Y \) confounded by elastic responses?**

In principle, elastic properties of cells and tissues affect the time-course of pressure responses. For example, substantial instantaneous and retarded elasticity was reported for excised coleoptiles of maize using extensiometer techniques (Hohl and Schopfer, 1992). In the experiments by Frensch and Hsiao, the direct determination of \( Y_1 \) and \( Y_2 \) in roots was particularly critical, because longitudinal shrinkage of the entire root would contribute to the growth recording using an LVDT. Frensch and Hsiao (1995) excluded a significant contribution of elastic longitudinal shrinkage for maize roots on the basis of experimental results on mature root tissue. Further evidence in favour of the correct determination of \( Y \) is derived from additional experiments on plants which include the elongation zone (Fig. 4). It can be seen that osmotic pressure steps in the absence of growth \((P_e < Y)\) did neither result in axial elastic shrinkage or swelling of the root. Radial elastic responses, which are likely to occur, would not contribute to the determination of \( Y \).

Besides mature xylem acting as a ‘backbone’ in the root, the experiments provide new evidence that a low water status of the tissue adds to the elastic response of the root. Shrinkage of the root could be induced during the later part of the experiment, when the nutrient solution was completely withheld from the root and \( P_e \) presumably dropped to zero (Fig. 4). Thus, elastic coefficients of single cortical cells in the order of a few MPa (Pritchard et al., 1990; Zhu and Steudle, 1991) may be useful to calculate radial elastic responses of roots, but are inadequate for longitudinal estimations. This relationship is extremely important for sustained uptake of water and nutrients. Significant changes in root length due to changes in water potentials in the xylem or soil would be expected to disrupt the contact between root and soil, established by root hairs and mycorrhizae. It is yet to be determined whether irreversible root extension in the basal part of the elongation zone is limited by the mechanics of progressively mature protoxylem in this zone. This proposition would differ from that postulated for stems and other aboveground organs, where growth appears to be limited by the expansion rate of the outer epidermis (Kutschera, 1995).

**The role of solute accumulation for adjustment of growth to water deficits**

The pattern of local growth rates along the elongation zone is associated with different rates of matter (water and solute) deposition (Sharp et al., 1988, 1990). Moreover, the adjustment of local root growth to moderate water stress \((\psi_m > -0.6 \text{ MPa})\) correlates with the ability of the root to maintain continuous solute uptake.
(Pritchard et al., 1991; Frensch and Hsiao, 1994, 1995). This is well illustrated by the different rates of turgor recoveries with respect to the amount of water deficits and to the position along the expansion zone (Fig. 5). At distances 4–5 mm behind the apex, \( \frac{dP}{dt} \) decreased by approximately one order of magnitude with increasing water stress (range of \( \Psi_m \): -0.1 to -0.6 MPa). It appears, therefore, that solute transport in the elongation zone is turgor-sensitive, as has been shown previously for carbohydrate transport in other tissues (Oparka and Wright, 1988; Patrick, 1994). At \( \Psi_m < -0.5 \) MPa, the turgor recovery in maize roots was confined to positions <7 mm (Frensch and Hsiao, 1995). The results imply that the shortening of the growing zone, which was also found by others (Sharp et al., 1988; Pritchard et al., 1993), was caused by the lack of solute accumulation to raise \( P_e \) above the minimum \( \gamma \) of 0.3 MPa.

Evidence for the phloem as the major source for solute accumulation is coming from different slopes of the turgor recovery at various positions in the cortex and from transient turgor gradients across the cortex at zero growth rates (Frensch and Hsiao, 1994). In these studies, the maximum rate of turgor recovery \( (\frac{dP}{dt})_{\text{max}} \) increased substantially from cells at the root periphery toward the endodermis. These experiments were carried out at zero growth rates, i.e. when dilution effects due to cell enlargement did not contribute to the effect.

Maximum rates of turgor recovery may be used to estimate the net deposition rates of osmotically active compounds into the elongation zone according to equation (6). For positions 4–10 mm behind the apex, an average \( \frac{dP}{dt} \) of \( 3 \times 10^{-4} \) MPa s\(^{-1} \) was evaluated for the cortex following a step change in \( \Psi_m \) from zero to -0.3 MPa (Frensch and Hsiao, 1995). Using measured root dimensions (radius of root = 400 \( \mu \)m, radius of stele = 150 \( \mu \)m) and assuming a value of 0.8 for the term \( \varepsilon/(\varepsilon + \pi_c) \) (Frensch and Hsiao, 1995), the net deposition rate into the cortex for an increment of 1 mm, \( \Delta n_c/\Delta t = 235 \) nosmol mm\(^{-1} \) length h\(^{-1} \) at \( T = 298 \) K. Accordingly, \( \Delta n_c/\Delta t = 785 \) and 118 nosmol mm\(^{-1} \) length h\(^{-1} \) for \( \Psi_m = -0.1 \) MPa and -0.6 MPa, respectively. Compared to maximum net deposition rates based on the evaluation of growth kinetics (Sharp et al., 1990), the data by Frensch and Hsiao were larger by factors of 2 to 5. It would be premature, however, to analyse the differences quantitatively from the present set of data. Nevertheless, they indicate that processes other than solute uptake may have contributed to the increase of \( P_e \) as well.

The coupling of solute transport and turgor adjustment in growing tissues has been investigated in hypocotyls of Ricinus (Meshcheryakov et al., 1992). Unlike roots, large radial turgor gradients were found which corresponded to a gradient in osmotic pressure of the same amount. Thus, the sum of both, the water potential, was essentially homogenous throughout the tissue. The results imply that solute transport from the center to the periphery is slow compared to water transport, and additional perfusion experiments supported the theoretical prediction that the regulation of the water potential in the symplast was very sensitive to small changes of the solute content in the apoplast (Steudle, 1992). The compartmentation of solutes between symplast and apoplast may also account for water potential gradients across the tissue, which are usually associated with the process of wall loosening (Cosgrove, 1993; Nonami and Boyer, 1993). More work is needed to understand the role of compartmentation in growing tissues.
and, especially, that of the apoplast within the complexity of tissue growth (Steudle and Frensch, 1996).

**What limits root growth?**

As already stated, limitations of growth are usually discussed in terms of hydraulic and mechanical resistances. The relative magnitude of the resistances can be estimated from the ratio (Boyer, 1985)

\[
\frac{mV}{LpA} = \frac{\Psi_m - \Psi_c}{P_c - Y}
\]  

according to the Lockhart theory. Values significantly smaller than 1 indicate a growth-limitation by the wall extensibility. Using measured values of \((P_c - Y)\) and calculated water potential gradients in growing maize roots (Silk and Wagner, 1980; Frensch and Hsiao, 1995), the ratio of mechanical versus hydraulic resistance ranges between 0.1 and 0.5 for unstressed and moderately stressed roots, depending on the axial and radial position of the expanding cell in the tissue. Cells at their maximum local growth rate, which make up most of the over-all growth rate, have values closer to 0.5, which suggests that both (or neither) of the parameters is rate-limiting.

It is tempting to argue that solute accumulation could have become the rate-limiting process for growth under water stress. In favor of this hypothesis are the possible pressure-sensitive distribution of carbohydrates and the close relationship between the reduced length of the elongation zone and the loss of turgor recovery (Frensch and Hsiao, 1995). Carbohydrates account for approximately 50% of the net solute deposition rate in maize roots (Sharp et al., 1990). They arrive from the shoot and are distributed radially into the growth zone along the symplastic route (Fig. 6). The flow rate of sugars decreases progressively with farther distance from the phloem until it eventually drops to zero in the epidermis. Simultaneously, water enters the tissue largely across the epidermis, driven by water potential gradients induced by either wall relaxation or solute gradients along the radial path. Under steady conditions, a 'functional equilibrium' is expected for this position, where the local growth rate is determined by cells limited in either carbohydrate or water supply. The ratio between the rate constants of water and solute flow would then determine whether the overall growth rate is closer associated with cell layers at the periphery or with those in the center of the root. With increasing water stress and lower levels of \(P_c\), the results in Fig. 5 suggest that the epidermis could become the growth-limiting cell layer in the root, provided that \((P_c - Y)\) can adjust to positive values. On the other hand; turgor recovered rapidly in cortical cells following small perturbations in the medium \((\Psi_m \geq -0.1 \text{ MPa})\). This indicates that there is no obvious limiting factor or tissue during steady growth conditions.

There is growing evidence that plasmodesmata represent the major resistance for symplastic solute flow (Bret-Harte and Silk, 1994). Dye-injection studies suggest that symplastic unloading from the phloem ceases when root growth is reduced (Oparka et al., 1995). Although the reduced permeability would explain the results presented in the present study, there is also evidence for the contrary. Using electron microscopy, Schulz (1995) reports a widening of plasmodesmata in pea roots in response to osmotic step changes in the medium, which would enhance symplastic solute flow at constant concentration gradients across the tissue. Perhaps, the lack of turgor recovery correlates with a smaller driving force for phloem unloading at low \(\Psi_m\), which requires further attention in future experiments. In either case, solute transport into the elongation zone appears critical for continuous root growth in water-stressed and unstressed roots.

**Growth limitations: scaling up from cell to organ level**

So far, the discussion on interactions between cell enlargement and water shortage has been confined to the
elongation zones of the root and leaf. Different plant organs, however, do not experience the same amount of water stress which relates to the observed differential growth responses of the two organs (Fig. 1). The gradients in water potential between the elongation zones in root and shoot largely depend on the hydraulics of the root system. Therefore, growth limitations as related to aspects of water transport in roots shall now be discussed.

Water loss of the plant to the atmosphere generates a tension in the xylem which, according to the cohesion theory, propagates into the root and reduces the water potential of the xylem below that of the soil. Limited by hydraulic resistances in series and parallel, water moves along the gradient from the soil to the shoot. It is useful, therefore, to separate the volume flow into a radial and an axial component. The longitudinal flow is solely driven by hydrostatic pressure gradients in the xylem. Within the radial pathway, water potential gradients may be hydrostatic, osmotic, or matric in nature. In the absence of transpiration, the osmotic gradient dominates, which leads to guttation and xylem exudation in many plants.

Radial water flow in roots is commonly analysed applying a two-compartment model in which the xylem is separated from the soil by a complex barrier (Passioura, 1988; Steudle, 1994; Steudle and Frensch, 1996). The application of the root pressure probe technique to roots of herbaceous and woody species has yielded the remarkable result that the radial hydraulic conductivity of the root \( L_p \) strongly depended on the nature of the driving force. In tree roots, for example, \( L_p \) (hydrostatic) was larger than \( L_p \) (osmotic) by one to three orders of magnitude, whereas no difference between \( L_p \) (hydrostatic) and \( L_p \) (osmotic) was found in Phaseolus and barley (Steudle, 1994). Radial volume flow rates in maize are larger by approximately one order of magnitude in the presence of hydrostatic pressure gradients compared to osmotic (Fig. 7). The experiments on plants of different age show that discrepancies between \( L_p \) (hydrostatic) and \( L_p \) (osmotic) were found consistently in young roots as well as in three-weeks old root systems, when the length of the main root axis exceeded 600 mm.

The data in Fig. 7 further illustrate a decreasing efficiency of roots in water uptake when the main axis exceeded a length of approximately 200 mm. This result is not surprising if one considers the developmental gradients along the root axis. From the apex toward the base, the function of the root shifts from a tissue more specialized in material uptake to one more specialized in material translocation. To some extent this process may be compensated by the development of laterals, although this effect appeared to be small in the present experiments on maize roots. For roots exposed to uniform environmental conditions, water uptake characteristics in hydrostatic experiments remained rather constant along the apical 150 mm. The decline of \( L_p \) (hydrostatic) by one order of magnitude coincided with the growth of root laterals, emerging from the cortex approximately 150 mm behind the apex. After 14 d in nutrient solution, when the main axis had reached lengths of approximately 500 mm, laterals accounted for more than 90% of the total root surface area (Frensch, 1990). Hence, small \( L_p \) of older roots largely represents the hydraulic conductivity of the laterals. It may be concluded that the laterals of maize roots grown in solution culture are less efficient in terms of water uptake and transport than the main axis.

Radial water transport in roots is composite in nature (Steudle, 1994). The corresponding model involves two parallel pathways: an apoplastic and a cell-to-cell path, each exhibiting different hydraulic and osmotic properties. It has been supported by pressure clamp experiments on Prunus using a different experimental and theoretical approach (Magnani et al., 1996). Despite its advantages, it is worth noting that this model simplifies the process of water transport in roots considerably. Root development and function depends much on the physical and chemical conditions of the immediate environment, which is largely unexplored for most plants under natural conditions (Waisel et al., 1991; McCully, 1995).

Both axial and radial resistances as well as water potential gradients vary with time and space along the root. The implications for the hydraulic architecture of the root have been studied theoretically and experimentally on excised and intact roots using pressure probe techniques (Frensch and
Pressure propagation across the root and implications for leaf and root growth

Information on soil water content is transmitted to the shoot by hydraulic and metabolic 'signals' originating in the root. They modulate stomatal movement and shoot growth within complex control loops (Tardieu and Davies, 1993). Over the past decade, the action of the phytohormone abscisic acid has been investigated extensively, whereas the meaning of the hydraulic component was largely neglected. To some extent, the negligence may result from the lack of appropriate techniques to measure and to modify xylem pressures in plants. Numerous measurements of xylem water potential by indirect methods (e.g. psychrometry, Scholander's pressure-chamber technique) have predicted substantial tensions in the xylem of a transpiring plant. Recent studies have yielded satisfactory results on the reliability of the pressure chamber technique, i.e. to correlate applied (positive) pressures with tensions in excised plant material (Holbrook et al., 1995; Pockman et al., 1995). Data of negative pressures in these studies are in accordance with the cohesion theory, which has prevailed the literature on water movement in plants over the last 100 years. However, the dogmas of this theory have been attacked on the basis of direct measurements in the xylem using a modified cell pressure probe (Balling and Zimmermann, 1990; Zimmermann et al., 1993). The authors report higher (less negative) values in the xylem of herbs and tree species compared to \( P_x \) obtained by the pressure chamber technique. Direct xylem measurements in trees indicated that longitudinal pressure gradients were too small to move water from the roots to the leaf by a purely hydraulic mechanism (Benkert et al., 1995). If true, the results of Zimmermann and co-workers would change basic concepts of the mechanism of long-distance transport in the xylem. However, the results have to be taken cautiously. Due to technical limitations of the cell pressure probe in the negative pressure range, which have not been addressed satisfactorily in the studies by Zimmermann and co-workers, the critique against the cohesion theory has been refused (Steudle, 1995).

The existence of longitudinal pressure gradients is a key feature of the cohesion theory and also relevant for plant growth. How effectively do pressure changes in the shoot propagate into the root and further into the soil? Recently, the propagation of hydrostatic pressures was measured in the cortex and in the xylem of maize root systems (Frensch and Hsiao, 1993; Frensch et al., 1996). These experiments provided novel results on the interactions between root structure and function. When the shoot was replaced by a modified root pressure probe, volume flows could be induced either into or out of the cut end of the excised root (Fig. 8). The cell pressure probe was used to scan the kinetics of the pressure propagation along mature and immature xylem (\( \Delta P_x \)) of root systems up to 500 mm in length. As expected, \( \Delta P_{app} \) was rapidly transmitted (fractions of a second) along conductive xylem. Longitudinal pressure propagation was determined from constant values of \( \Delta P_x \) and \( \Delta P_{app} \). Ratios of \( \Delta P_x/\Delta P_{app} \) ranged from values close to 1 at the base of the root to almost zero at the root tip (Frensch et al., 1996). Based on measured \( \Delta P_x/\Delta P_{app} \), a hypothetical pressure profile was calculated for the boundary condition \( P_x = -0.5 \text{ MPa} \) at \( z = 500 \text{ mm} \) and \( \psi_m = 0 \text{ MPa} \) (closed symbols in Fig. 8). The data show that a tension in the shoot is maintained for a long distance in the root xylem, but steeply attenuates toward zero in the apical 200 mm.

The attenuation of xylem pressure is important for the differential growth of roots and shoots in the presence of water deficits in the atmosphere and in the soil. In our example, the leaf elongation zone would experience a tension in the xylem (apoplast) of \(-0.5 \text{ MPa}\) or less, while \( P_x \) in the root elongation zone would be almost zero. Frensch and Hsiao (1993) concluded that root elongation was rather hydraulically isolated from changes in water potential that originate in the shoot. On the contrary, water potential gradients along the root are different when water stress is imposed through osmotic changes in the medium. In the absence of significant transpiration, the osmoticum reduces \( P_x \) more evenly over the entire length of the root. Due to reflection coefficients of the root smaller than unity, values of \( \Delta P_x \) are smaller than the corresponding \( \Delta P_{app} \) (Steudle and Frensch, 1989). Hence, root growth is probably more affected than shoot growth when \( \psi_m \) is altered.

Assuming that transpiration is the major driving force for water transport, the experiments on pressure propagation along the xylem resemble the situation in the intact plant. Further steps toward an understanding of dynamic pressure changes in the xylem under transpiring conditions require direct measurements in the xylem. These experiments were performed on plants kept in either solution culture or in soil (Frensch, Dieffenbach and Göttlein, unpublished results). Reliable tests of the cell pressure probe along with further control experiments demonstrated convincingly that the measurements were performed in conductive xylem. Negative xylem pressures of down to \(-0.5 \text{ MPa}\) absolute were recorded in roots of maize plants. They depended not only on transpirational water loss, but also on the availability of water in the medium and soil. Essentially, the results verified that transpiration generates a rapid and effective driving force for water uptake in the xylem. Furthermore, the studies explain the apparent lack between transpiration and xylem pressure, which was used by Zimmermann and
Fig. 8. Experimental set-up and results of longitudinal pressure propagation on excised roots. With the syringe detached, the root pressure probe recorded steady root pressures of maize roots. Once the syringe was introduced, the pressure in the probe was clamped to a smaller or higher level than root pressure by means of compressed air. The arrows illustrate the directions of water flow following a pressure application higher than root pressure ($\Delta P_{\text{app}}$); the thickness of the arrows indicate that radial and axial flow varies along the main axis. The direction of flow could be reversed when $P_{\text{app}}$ in the probe was clamped to a value below the original root pressure. The bars to the left of the root axis indicate the zones of xylem maturation (PX = protoxylem; EMX = early metaxylem; LMX = late metaxylem) which affected the longitudinal pressure profile shown to the right. Throughout the root, pressure response ($\Delta P_x$) in mature (conductive) EMX and immature LMX was monitored with the cell pressure probe. Measured ratios of $\Delta P_x/\Delta P_{\text{app}}$ were multiplied by $\sim 0.5 \text{ MPa}$ (closed symbols) to illustrate a hypothetical steady profile for a transpiring plant. The profile indicates that pressure attenuation toward the tip 'isolates' the root elongation zone hydraulically from changes in xylem tensions generated in the shoot. The solid line was modeled using measured hydraulic resistances for axial and radial water transport determined by the root pressure probe technique according to the cable theory (see text). (Adapted from Frensch, 1990 and Frensch et al., 1996.)

In summary, when restricted to purely hydraulic aspects, the results indicate that root elongation is strictly coupled to the water potential of the immediate external surrounding. Shoot growth, on the other hand, is closely linked to changes in air humidity, provided that significant changes in $P_x$ are induced by transpiration. If the phloem is included in these considerations, root elongation may also respond immediately to hydraulic changes in the shoot. It is common to consider that carbohydrate flow into the sink region depends on a hydrostatic pressure gradient along the phloem, which would be diminished by a rapid decline of water potential in the shoot, at least transiently. As discussed before, carbohydrate supply appears to be a critical factor for the rate of root elongation, especially when turgor in expanding cells is low.

Modelling of water potential gradients along the xylem

What caused the observed pressure attenuation in the root? This leads to a two-dimensional mathematical model of water flow in roots, adapted from a model of electric current flow along a leaky cable ('cable theory'; Taylor, 1963). The spread of nerve impulses along an axon is a more prominent example of the application of this theory (Rall, 1987). It extends the two-compartment (one-dimensional) analysis of water uptake introduced before by a longitudinal flow in the xylem. Applied to roots, the cable theory predicts gradients of longitudinal xylem pressure on the basis of two parameters: radial ($R_r$) and axial resistances ($R_x$). Assuming constant values of $R_r$ and $R_x$, the equations of the cable theory can be solved analytically (Landsberg and Fowkes, 1978). To model pressure profiles and cumulative flow rates in roots more realistically, the variable nature of hydraulic...
resistances was incorporated in the theory (French and Steudle, 1989; French, 1990). Using the root pressure probe technique to evaluate $R_e$ and $R_X$ (French and Steudle, 1989; French, 1990), the pressure attenuation along the xylem was modeled for the maize root system (Fig. 8, solid line). Similar pressure profiles were calculated for roots of Agave and Opuntia (Alm et al., 1992). It can be seen in Fig. 8 that the two independently determined profiles correspond reasonably well. Discrepancies between the profiles are probably due to the fact that the model (i) neglects the distribution of resistances within the laterals (largely unknown), and (ii) overestimates the contribution of axial resistances in the tip region (0–20 mm), which is difficult to assess with the root pressure probe.

According to the cable theory, the ratio $R_e/R_X$ is a fundamental parameter for the longitudinal pressure gradient in the xylem and, hence, for the distribution of water potential differences between the xylem and the root surface. An increase of $R_X$ would be associated with a higher proportion of immature xylem. Because resistances decrease with the forth power of the vessel radius, changes of $R_X$ due to xylem maturation are huge. With the differentiation of the early and late metaxytem, $R_X$ decreased by 5 orders of magnitude in maize roots (French, 1990); changes in $R_X$ by 3 orders of magnitude were reported for onion roots (Melchior and Steudle, 1993). Both studies emphasize to measure $R_X$ rather than to estimate this parameter from Poiseuille’s law because of significant differences between the two approaches. Changes in $R_X$ along the main root axis are affected by changes in both the apoplastic and cell-to-cell path. In older parts of grass roots, the endodermis is a likely candidate for the radial hydraulic barrier (Sanderson, 1983; McCully and Canny, 1988). The dominating role of the endodermis for radial as well as axial pressure attenuation was demonstrated for maize roots (Frensch et al., 1996). The results are consistent with measurements of water uptake in various root zones of barley and spruce (Sanderson, 1983; Häussling et al., 1988). Within the radial pathway, the lateral walls of mature vessels may also pose a significant resistance to water uptake (Peterson and Steudle, 1993), whereas the contribution of developmental changes in the hypodermis appears to be rather small (Clarkson et al., 1987).

Taken together, experimental data on pressure propagation in the xylem and cortex validate predictions of the cable theory. The model provides a sound basis to study the relationship between root structure and function at a mechanistic level. Future work should aim to include root growth and the responses of growth to water stress as well.

Conclusions

It has been known for a long time that cell expansion is extremely sensitive to changes in plant water potential, and that growth recovers rapidly from mild and moderate water stress. Recent progress toward a better understanding of the underlying processes is highlighted by this review. Measurements ranging from the cell to the organ level emphasize to study growth responses of plants at both high spatial and temporal resolution. The results confirm the fundamental relationship between turgor and cell expansion, which is usually masked when conventional approaches are applied, i.e. when steady conditions of turgor and growth are compared. In the past, this has led to confusion about the meaning of turgor for cell enlargement.

Evidence is presented that rapid modifications of the yield threshold as well as turgor-dependent solute transport into the growth zone are important features of roots during the process of adjustment. From these data it should be clear that growth and its recovery from transient inhibition is closely linked to solute transport. An adequate model of tissue expansion, which is still missing, should include pathways, mechanisms, and amounts of matter supplied by different compartments.

The differential responses of root and shoot growth are related to longitudinal water potential gradients in the plant. The attenuation of xylem pressure in roots is readily explained by the ‘cable theory’. It combines features of root structure (hydraulic resistances) and root function (water transport) and demonstrates that the elongation zones in the root and shoot of maize are hydraulically separated, consistent with previous experimental results. The data emphasize the need to study interactions between growth and water relations on a whole plant level.

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