Soil solute concentration and water uptake by single lupin and radish plant roots

II. Driving forces and resistances

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Abstract

Soil water extraction (Q) and the corresponding values of matric (Ψ_m) and osmotic (Ψ_π) potentials near single roots of eighteen day old lupin and radish plants, subjected to two levels of transpirational demand and five Na^+ soil solution concentration levels, were determined using a combination of computer assisted tomography applied to gamma and X-ray attenuation measurements and Na^+-LIX microelectrodes. This data together with leaf water potential (Ψ_l) measured by psychrometer, were used to calculate the differences in total water potentials ($\Delta\Psi$) and the differences in hydrostatic pressure (ΔP) between the leaves and the total potentials at the root surfaces, and to estimate soil and plant resistances to water movement. The linear relations for $\Delta\Psi(Q)$ and $\Delta P(Q)$ observed, imply that both plant roots acted as near perfect osmometers under the conditions of the experiments. This is further supported by the close agreement between the increases in ΔP and the decreases in Ψ_π at the root surface with increasing solute concentration in the treatments. Plant resistances were constant with time of transpiration and increased with increasing Na^+ in the treatments. Soil resistances between the root surface and bulk soil increased as the water content decreased remaining lower at the higher solute concentrations due to the lower extraction rates. At the high water potentials used plant resistances were always substantially higher than corresponding soil resistances.

Introduction

The rate of water flow from the soil to the plant is controlled by the total water potential difference along the pathway as expressed in Equation 1:

$$Q = \frac{\Psi_s - \Psi_m}{R_s} = \frac{\Psi_t - \Psi_l}{R_p} \qquad (1)$$

where Q is the transpiration rate, Ψ_s is the matric potential in the bulk soil, Ψ_m is the matric potential at the root surface, Ψ_t is the total water potential at the root surface, Ψ_l is the leaf water potential and R_s and R_p are the soil and plant resistances respectively.

Equation 1, which is based on an analogy with Ohm's law (Van den Honert, 1948) expects a linear relationship between Q and the driving force whether the driving force arises from the difference in hydrostatic pressure, ΔP, or in the total water potential, $\Delta\Psi$, between the root surface and the leaves assuming the plant resistance to be constant. This is not always the case (Janes, 1970; Millar et al., 1971). In theory all components of equation 1 (i.e. Q, $\Delta\Psi$, and R_p)

should vary depending on their location of measurement in a branched system such as a plant (Richter, 1973). Cowan (1965) and Noble (1974) have discussed the mechanistic connection between $\Delta\Psi$ and Q and agree that to satisfy the linearity between the driving force and Q, the flow of water should be liquid not vapor, the system should be isothermal, the plant resistance should be independent of any component of the water potential and there should be no solute flow in the system.

When a plant root is exposed to a saline solution in the soil, the water potential at the root surface is lowered. This decrease is transmitted throughout the plant and the extent of the transmission can be described in terms of the overall apparent hydraulic resistance of the plant and the rate of water flow through the plant (Equation 1). Changing its root resistance enables the plant to satisfy the transpirational demand without developing undue stress by steeply lowering its leaf water potential (Shalhevet et al. 1976). Such changes usually occur either when the soil moisture is depleted or when a substantial amount of salt is present in the soil. However both Dalton et al. (1975) and Fiscus (1975) showed that non-linearity in the relationship between Q and the driving force does not necessarily imply that R_p varies, but it may imply that solutes are involved in driving the flow of water.

Passioura (1984) questioned whether the non-linearity was real at the fundamental level, whether it arose merely because of inadequate measurements of flow rates or driving force or whether it was caused by the involvement of solutes in driving the flow of water as claimed by Dalton et al. (1975) and Fiscus (1975). Fiscus et al. (1983) had argued that the time had come to abandon the analogy with Ohm's law and use instead other equations derived from irreversible thermodynamics. The relative magnitudes of soil and plant resistances to water movement under different conditions of soil water potential and transpirational demand, have also been the subject of some debate (Newman, 1969; So et al., 1976a,b).

The controversy surrounding these considerations arises from the fact that the driving force which moves the water from the root surface to the leaves involves some components which have

been difficult to measure by conventional techniques. In the present paper, data for water uptake and solute accumulation obtained using an innovative combination of computer assisted tomography applied to X- and gamma-ray attenuation (CAT scanning) and sodium-liquid Ion exchanger (Na^+-LIX) microelectrode techniques (Hamza and Aylmore, 1992), has been used to examine the relationships between the driving forces, rates of water uptake and soil and plant resistances for single lupin and radish plant roots.

Materials and methods

Application of Computer Assisted Tomography CAT to gamma and X-ray attenuation measurements (Hainsworth and Aylmore, 1983, 1986, 1988) was used to determine the spatial distribution of soil water content and hence water uptake by individual root layers of eighteen day old plants subjected to two levels of transpirational demand (with and without a fan) and five Na^+ concentration levels (zero, 25, 50, 75, and $100 \, mol/m^3$) at initial soil water contents of $0.3 \, cm^3/cm^3$. These were monitored at three root depths of 3, 6 and 9 cm and at zero, 2, 4, 6 and 8 hour intervals from the commencement of transpiration. Na^+-LIX microelectrodes were used, in situ, to determine Na^+ concentrations at the root surface with time of transpiration. For this purpose soil pots were specifically designed and constructed to allow accurate positioning of the microelectrode tips at the root surface (Hamza and Aylmore, 1991). Full details of the experimental methods used have been presented in the preceding paper in this series (Hamza and Aylmore, 1992).

Results and discussion

Graphs illustrating the experimental data for the changes in the spatial distribution of soil water content (i.e. drawdowns) and Na^+ ion concentrations in proximity to the lupin and radish plant roots for the five Na^+ concentration levels and two rates of transpirational demand with time of transpiration, were presented in Part I

(Hamza and Aylmore, 1992). The values of the instantaneous transpiration rate, Q, after 2, 4, 6 and 8 hours of low and high transpiration demands were calculated as the first derivatives of the third degree polynomial curves fitted to the values of the cumulative water uptakes vs. time. The corresponding values of Ψ_m and Ψ_π at the root surfaces and leaf water potentials Ψ_1, were obtained from CAT scanning, Na^+-LIX microelectrode and leaf psychrometer data respectively. The total water potentials at the root surface, Ψ_t were calculated as the sum of the matric and osmotic components.

Driving forces

The relationships between the values of $\Delta\Psi$, the differences in water potentials between the leaves and the total potentials at the root surfaces, which constitute the driving forces for transpiration, and rates of water uptake (Q) were essentially linear (Fig. 1). In all cases as transpiration progressed, leaf water potentials and total water potentials at the root surfaces decreased but both the differences in water potentials between the leaves and root surfaces and the transpiration rate increased.

The relationships between the transpiration rate, Q, and the difference in hydrostatic pressure between the root surface and the leaves, ΔP, were also linear for both the lupins and the radishes subjected to both low and high transpiration demands (Fig. 2). ΔP in this experiment was calculated as the difference between Ψ_m at the root surface and the water potential at the leaves, Ψ_1, for the transpiring plants. Strictly speaking ΔP calculated in this fashion includes changes in osmotic component of the leaf cell walls. However further consideration demonstrated that this component is essentially constant (Munns and Passioura, 1984). This is true if the root membranes act as near perfect osmometer.

Steudle and Jeschke (1983) have suggested that the active uptake of ions into the root xylem provides some of the gradient of water potential for the absorption of water from the soil and the interaction between solute and water flow plays an important role in the water relations of the root. Based on the theory of coupled flow of
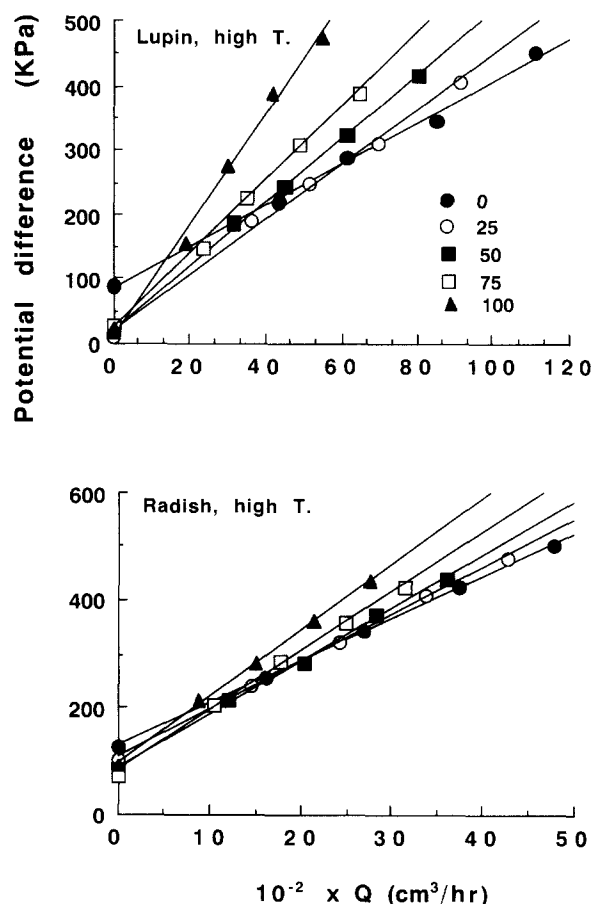

Fig. 1. The relationship between $\Delta\Psi$ and Q for the lupin and radish plants subjected to high transpiration demand and solute treatments of 0, 25, 50, 75 and 100 mol m^{-3} Na^+. The osmotic component at the root surface was measured using Na^+-LIX.

solute and water across a semipermeable membrane (Katchalsky and Curran, 1965) ion uptake should be related to water uptake. Both Dalton et al. (1975) and Fiscus (1975) using an equation derived from irreversible thermodynamics, have suggested that non-linearities do not necessarily imply that the plant resistance varies, but rather that solutes are involved to varying extents in driving the flow of water. Conversely it has been argued (Cowan, 1965; Nobel, 1974) that for linearity between Q and the driving force to be satisfied, no solute flow into the plant should occur.

The numerical values of ΔP (Fig. 2) were invariably much higher than the numerical values of the osmotic potential at the root surface (see
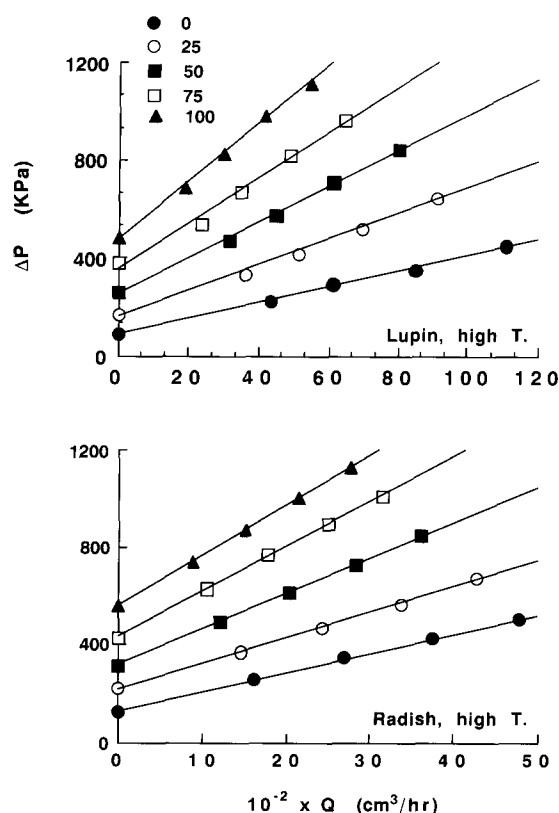
Fig. 2. The relationship between the hydrostatic pressure difference between the lupin and radish root surfaces and leaves (ΔP) and the high transpiration rates (Q) for solute treatments of 0, 25, 50, 75 and 100 mol m^{-3} Na$^+$.

Hamza and Aylmore, 1992). Thus the restriction on the flow of water imposed by the osmotic potential at the root surface, is far exceeded by the hydrostatic pressure difference between the root surface and the leaves. Although appreciable amounts of solute are present at the root surface this clearly fails to produce any noticeable curvature in the $\Delta P(Q)$ or $\Delta\Psi(Q)$ curves presumably due to the high values of ΔP. Similar near-linear increases in sap flow rates with applied pressure have been reported by Nulsen and Thurtell (1978) for well watered detopped maize root systems exposed to as low as -380 kPa osmotic potential when their values for ΔP were higher than the numerical values of the solution osmotic potential. However when the applied pressure was less than the numerical value of the solution osmotic potential the exudation rate was a curvilinear function of the applied pressure.

Similarly Passioura (1980) observed that when the soil was wet, the relationship between Q and the driving force was linear, but as the soil dried, non-linearities appeared. ΔP in both these experiments was imposed on the plants using a pressure chamber technique. Although the principle is theoretically the same, an artificial driving force may not necessarily act in exactly the same fashion as one produced by the transpiring plant. In wet soil, especially in sandy soil such as that used here, soil resistance to flow is essentially negligible and almost no restrictions are imposed on water flow towards the plant. In such conditions a linear relationship would be expected to occur between the flow of water and the driving force provided that most osmotica are excluded at the root epidermis. In this experiment the initial water content was high (0.30 cm^3 cm^{-3} $\equiv -33$ kPa) and the lowest Ψ_m value at the root surface at the end of the transpiration period was -140 kPa. This value is not low enough to restrict water availability to the plant. Thus the linearities observed in the present data indicate that either no NaCl was taken up by the plants or that any NaCl taken up had no significant influence on the water driving force. If absorption of salts occurs the amount is small and this has presumably been largely swept away from the root xylem by the transpiration stream.

The intercepts of $\Delta P(Q)$ on the ΔP axis, ΔP_0 (Fig. 2) correspond to the threshold values of the driving force necessary to begin flow through the system and reflect the differences in the osmotic pressure across the root, $\Delta\Psi_\pi$. ΔP_0 values differ only slightly from the ΔP values obtained from CAT and psychrometer data for the no flow situation (Table 1) in accord with the linear relations observed. The values of ΔP_0 obtained for the "no solute" condition undoubtedly reflect the presence of salts naturally occurring in the soil matrix prior to the saline irrigation treatments and agree very closely with the values of osmotic potential obtained by LIX at zero time. The close values between the decreases in Ψ_π and the increases in ΔP_0 with increasing solute concentration in the treatments (except for the lowest solute treatment) indicates a near-perfect osmotic behaviour by the lupin and radish roots over this range.

Table 1. Values of Ψ_π at the root surface at zero time of transpiration, ΔP_0, the decrease in Ψ_π and the increase in ΔP_0 with increasing solute treatments for the different solute treatments and transpiration (low/high) demand, for the lupin and radish plants

Treatments Na$^+$ mol m^{-3}	Ψ_π $-$kPa	ΔP_0 kPa	Decrease in Ψ_π (kPa)	Increase in ΔP_0 (kPa)
Lupin, Low transpiration				
0	–	81	–	–
25	117	149	117	68
50	236	245	119	96
75	356	364	120	119
100	467	472	111	108
Lupin, High transpiration				
0	–	84	–	–
25	117	155	117	71
50	234	248	117	93
75	355	351	121	103
100	467	469	112	118
Radish, Low transpiration				
0	–	128	–	–
25	118	216	118	88
50	234	308	116	92
75	355	430	121	122
100	464	546	109	116
Radish, High transpiration				
0	–	128	–	–
25	116	215	116	87
50	236	316	120	101
75	355	431	119	115
100	467	557	112	126

The correct interpretation of Ψ_l is of vital importance in determining the true water potential gradient through the plant because the plant hydraulic system itself acts as a continuum (Nulsen et al., 1977) and any fall in water potential at the root surface, such as occurs when the root system is exposed to osmotica, is transmitted through the plant. To describe such transmission, i.e. by applying Ohm's law analogue, the water potential of the leaf cytoplasm should be used rather than the water potential of the cell walls as is usually measured by using a psychrometer. However it can be assumed that if zero or only small amounts of solute are flowing with the water to the leaves, the psychrometer values can be regarded as representing, to a large extent, the true values of the leaf water potential. Even though, both driving forces, ΔP and $\Delta \Psi$, showed linear relationships with Q, it is suggested that $\Delta \Psi$ is the better measure of the

driving force between the root surface and leaves than ΔP, because it takes Ψ_π at the root surface into account.

Soil and plant resistances

Plant hydraulic resistances R_p for the lupin and radish plants, obtained from the slopes of the $\Delta \Psi(Q)$ plots, and the corresponding soil resistances, calculated from Q and the differences between potentials at the root surface and bulk soil, for the different solute treatments and transpiration intervals are compared in Fig. 3. In the present experiments both Ψ_π and Ψ_m values at the lupin and radish root surfaces were measured simultaneously at about 4 cm below the soil surface and were assumed, for the purpose of calculating R_s and R_p, to be constant along the root length.
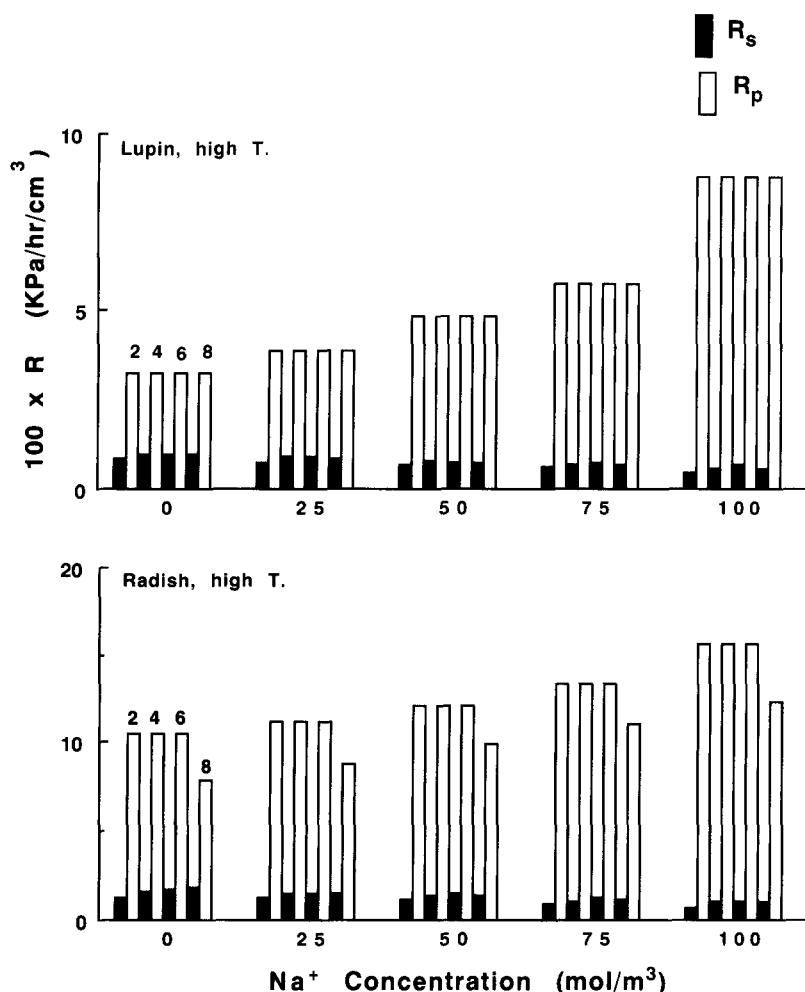
Lupin plant resistances, R_p, ranged from 3 to

Fig. 3. Soil and plant resistances for the lupin and radish plants for solute treatments of 0, 25, 50, 75 and 100 mol m^{-3} Na$^+$ after 2, 4, 6, and 8 hours of high transpiration demand.

15 times higher than the corresponding soil resistances, R_s, and from 4 to 12 times higher in the case of the radish plants depending on the solute concentration and transpiration period. As transpiration progressed and the soil around the root surface dried, R_s increased slightly while R_p remained constant (Fig. 3). Thus the differences between the plant and soil resistances decreased with time of transpiration. While plant resistances increased with increasing solute concentration in the treatments, soil resistances decreased mainly because less water was taken up by the plant and thus the soil remained wetter. Consequently the difference between R_p and R_s increased with increasing solute concentration in the treatments.

The results showed clearly that soil resistances were much less significant than plant resistances under the soil moisture conditions occurring in these experiments. This is consistent with Newman's (1969a,b) suggestion that at high water contents soil resistance is less significant than plant resistance and that only as the soil dries out (e.g. at Ψ_m around -1500 kPa), does soil resistance increase and become the predominant component of the total resistance. In the present experiments the values of Ψ_m at the root surface or at any point throughout the soil never fell below -140 kPa which is clearly far from the wilting point. Burch (1979) for example, found that a large and almost constant plant resistance influenced the pattern of water absorption until

the soil resistance reached about 1.5×10^3 MPa s cm^{-3} which corresponded to an extraction of almost 80% of the available soil water. Reiscosky and Ritchie (1976) found that the plant resistance was much larger than the soil resistance until the potential was reduced below -100 kPa. The previous workers dealt mainly with whole root systems rather than with single roots and hence Gardner's approach would be less relevant. Other workers have similarly reported that soil resistance is seldom large enough to contribute significantly to the overall resistance (Campbell, 1985) and that the major resistances are within the plant (Ehrlers et al., 1981; Samui and Kar, 1981). In contrast to the above, Gardner (1960) and Carbon (1973) have suggested that the conductivity of soil to water can often be so small that the transport of water to

the plant root may limit uptake even when much available water remains in the soil. Similarly Hulugalle and Willatt (1983) using data for soybean concluded that the soil resistance may be more significant than that of the plant at relatively high water contents.

The nature of the data presented here does not make it possible to differentiate between radial and axial resistances in the plant root. However the values of Hounsfield units (H) (Hamza and Aylmore, 1992) across the lupin root (Plate 1) are clearly much higher (i.e. more dense) across the cortex region of the root than in the stele region. For example the value of H units for the stele of 109 increases progressively over 0.5 mm intervals away from the stele toward the root surface, to 203, 300, 410, 500, 611 then to 725 almost at the root surface. Increasing
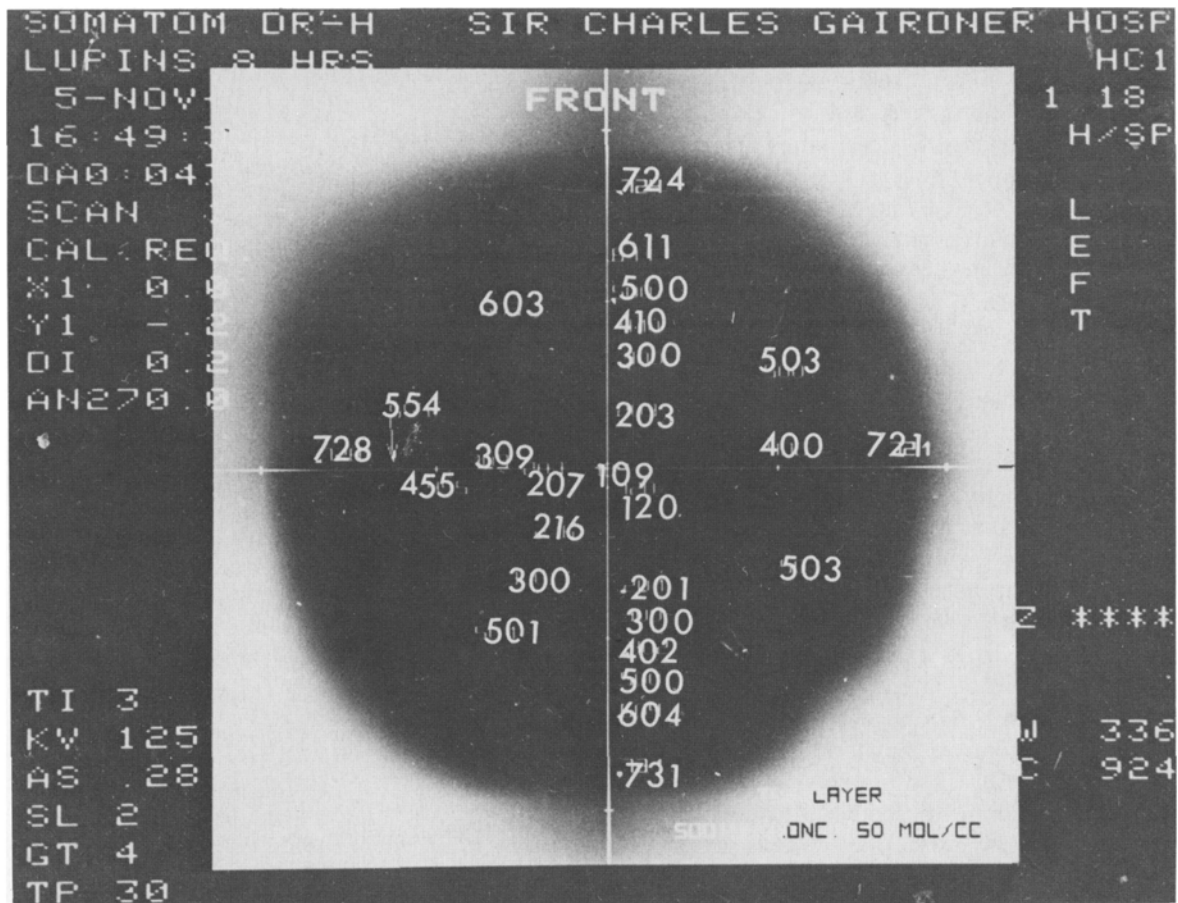

Plate 1. Hounsfield unit values through a cross-section of a lupin root. The root diameter is approximately 4 mm.

values of H units correspond to increasing density of the media (H unit for water is zero or slightly lower). Increasing values of H units toward the root surface may thus indicate higher radial resistance to water flow than that for the stele. If so the radial root resistance would be more important than the axial root resistance in controlling the water flow along the plant root. This suggestion agrees with the published results on the importance of radial root resistance over the axial resistance (Burch, 1979; Oosterhuis, 1981; Rowse and Goodman, 1981).

Plant resistances under the low transpiration demand were higher than those obtained under the high transpiration demand by about 150 to 200 kPa hr cm^{-3} for the lupins but the reverse occurred in the case of the radish plants where R_p values under the high transpiration demand were about 60 kPa hr cm^{-3} higher than those observed under the low transpiration demand. However these differences were small and the radish R_p can be regarded as near constant. It may be that the difference in R_p between the lupin and radish plants is related to the geometry of the plant root which determines the water absorbing area and radial and axial resistances. It is commonly observed that as the transpiration rate increases plant resistance decreases (Macklon and Weatherley, 1965, for castor bean; Stoker and Weatherley, 1971, for cotton and sunflower; Barrs, 1970, for tomato and maize).

Values of R_p for the radishes were higher than those for the lupins by about 1.5 to 2.5 times. This is to be expected because the total root surface area of the radish single root is much smaller than that for the lupin. This means less radish root surface area is in contact with the soil water as compared with the lupin root. Also, in contrast to the lupin root, the radish root radius and presumably the xylem is much smaller which gives it a much higher axial resistance. Furthermore the radish root radius decreases along its length (i.e. from 0.035 cm at the top layer to 0.230 and 0.090 cm at the middle and bottom layers respectively). This possibly increases the axial resistance along the roots. Although both lupin and radish roots were never water-stressed, if, within the range of soil moisture encountered in this experiment, any root shrinkage occurs, then the effect of loosing root hydraulic contact

with the soil (Herkelrath et al., 1977; Huck et al., 1970) will be much greater for the radishes. Such effects may cause a large increase in radish root resistance. However the magnitude of the plant resistance varies considerably from plant to plant even within a single cultivar of one species.

Conclusions

The linear relations for $\Delta\Psi(Q)$ and $\Delta P(Q)$ observed here imply that both plant roots acted as near perfect osmometers under the conditions of the experiments. This is further supported by the close agreement between the increases in ΔP and the decreases in Ψ_π at the root surface. A particularly interesting and important extension of the present studies would be the use of the microelectrode technique developed here to study simultaneous (and preferably in conjunction with the CAT technique) the ionic concentrations both within the root xylem and outside the root and the changes which occur as the soil solution concentration increases. Plant resistances were constant with time of transpiration and increased with increasing Na$^+$ in the treatments. Soil resistances between the root surface and bulk soil increased as the water content decreased remaining lower at the higher solute concentrations due to the lower extraction rates. At the high water potentials used plant resistances were always substantially higher than corresponding soil resistances. More information is needed on the role which water potential gradient along the roots plays in the redistribution of water and solutes and how this changes with overall soil water potential.

Acknowledgements

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