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Communication

Effects of Sodium Chloride on the Hydraulic Conductivity of Soybean Root Systems[1]

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ABSTRACT

Root system hydraulic conductivity (L_p) was measured on soybean (*Glycine max* [L.] Merr. var Harosoy) seedlings grown in solution culture and exposed to varying levels of osmotic stress. Hydroponic growth solutions were salinized by additions of NaCl, and the permeability of excised seedling root systems to water was measured. Conductance was estimated at high rates of water flux, where osmotic effects are negligible. L_p was reduced as the salinity of the growth solution increased. Growth in NaCl for 14 days at −0.17 megapascals and −0.26 megapascals resulted in reductions in L_p from that of controls by 27% and 72%, respectively. L_p was correlated with the root/shoot biomass ratio (*RS*), with larger values of L_p observed in seedlings with lower *RS*.

The volume flow of water, J_v[2], between any two points in a diffusion-limited hydraulic system is related to the driving force by

$$J_v = L_p(\Delta P + \sigma\Delta\pi)$$

where L_p is the hydraulic conductivity (cm s^{-1} MPa^{-1}) of the membrane and σ is its reflection coefficient, and ΔP and $\Delta\pi$ are the differences in hydrostatic pressure and osmotic pressure, respectively, between the two points (1). L_p is a parameter of significant biological importance because it defines the ability of a tissue to supply water to growing cells. Although it is a critical variable in models of water uptake, water balance, and plant growth, considerable uncertainty exists with regard to how it may be modified by the salt concentration of the root media (8, 10, 11, 14).

The magnitude of L_p determines, for a given flow rate, the size of the water potential gradient between growing and absorbing regions. Any decrease in L_p brought about by exposure to saline media would act to steepen the water potential gradient that would otherwise be necessary to sustain water flow.

The salt concentration of root media is known to affect plant water status and leaf expansion of nonhalophytes, and Munns and Termaat (9) suggested that the water status of roots is probably the most important factor regulating leaf expansion during short-term exposure to salinity. However, due to the technical difficulties involved in estimation of L_p, few studies have been conducted to test the effects of root media salinity on the hydraulic properties of plant roots.

The objective of this experiment was to characterize changes in soybean root system L_p induced by exposure to osmotic stress. Hydroponic growth solutions were salinized by additions of NaCl, and the permeability of excised seedling root systems to water flow was measured. Conductance was estimated at high rates of water flux, where osmotic effects are negligible.

MATERIALS AND METHODS

Soybean (*Glycine max* [L.] Merr. var Harosoy) seedlings, germinated in June 1988 and grown for 7 d in sifted Peat-Lite, were transferred to a flow-through hydroponic system, filled with single-strength Hoagland solution (5). Seedlings were mounted singly in the lids of sealed, 1-L containers which were supplied with circulating nutrient solution from 20-L reservoirs. Six treatments were applied by varying the NaCl concentration in the reservoirs, and solution osmotic potential was measured with a Wescor model 5100CXR vapor pressure osmometer (Wescor, Logan, UT). Treatments included Hoagland solution without added NaCl (−0.10 MPa) and five levels of solution osmotic potential (−0.13, −0.17, −0.20, −0.23, and −0.26 MPa). Solution pH was adjusted to 5.5 and readjusted daily for each treatment. Five treatment replications were included in this design. Plants were grown on a greenhouse bench with maximum day temperatures of approximately 27°C and minimum night temperatures of approximately 23°C. After 14 d of growth, five seedlings were harvested at random from among the treatments and prepared for determination of root system hydraulic conductivity. Five additional seedlings were harvested and analyzed each day until the experiment was completed 4 d later.

The experimental procedure for L_p estimation was similar to that described by Markhart *et al.* (7). Root systems were severed immediately above the cotyledon leaf scars and sealed in a stainless steel pressure chamber with the cut stump protruding through a rubber gasket. The chamber, containing 40 L of Hoagland solution, was pressurized with compressed

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[2] Abbreviations: J_v, volume flow of water; L_p, root system hydraulic conductivity; *C*, plant hydraulic conductivity; *E*, transpiration; ΔP, hydrostatic pressure difference; *RS*, root/shoot biomass ratio; Ψ_{leaf}, leaf water potential; Ψ_{soln}, solution water potential.

air, and a rotameter regulated flow and allowed for constant aeration of the solution.

After root systems were sealed in the lid, chamber pressure was gradually increased to 0.27 MPa and held constant until flow rate, *Q*, became stable. Water expressed from each cut stump was delivered via tygon tubing to a system of computer-controlled valves and partitioned such that the exudate from one root system at a time was weighed by an electronic balance. *Q* was computed every 4.75 min, and valves were automatically switched to allow sequential data collection from each of five root systems. Flow rates were logged for 100 min at each of four applied pressures (0.21, 0.28, 0.34, and 0.41 MPa), allowing 5 min equilibration periods between pressures.

Upon completion of the exudation measurements, root systems were removed from the chamber, and secondary roots were severed from the main tap root. The total length, *l*, of each root system was estimated by use of an image analyzer (Decagon Devices, Pullman, WA), after staining with methyl violet. L_p was estimated after making the assumption that the root can be considered, to a first approximation, a cylindrical membrane system with radius *r* (3). Although the value of the effective membrane radius in relation to root anatomy is still somewhat controversial, it was further assumed that the membrane is coincident with the endodermis. Because a preliminary analysis of the distribution of root radii among treatments revealed no consistent differences in root thickness among salinized and control plants, an approximate radius of 0.2 mm was taken, and the effective endodermal membrane surface was estimated by $2\pi rl$. J_v was computed by transforming *Q* to reflect total flow on the basis of root membrane surface areas, and L_p was estimated as the slope of the regression of J_v on applied hydrostatic pressure.

RESULTS

Figure 1 displays the volume flux of water as influenced by applied hydrostatic pressure for two representative seedlings, one grown in single-strength Hoagland solution ($\Psi_{soln} = -0.10$ MPa) and the other in solution to which NaCl had been added ($\Psi_{soln} = -0.20$ MPa). L_p was estimated for each seedling as the slope of the regression of J_v on ΔP; the R^2 values for individual regressions typically were between 0.97 and 0.99. L_p varied between approximately 2.0 and 7.0×10^{-5} cm s^{-1} MPa^{-1}, depending on the severity of osmotic stress.

L_p was estimated for each seedling root system in each of the six salinity regimes, and mean values are plotted against Ψ_{soln} in Figure 2. Increasing the salinity of the growth solution by addition of NaCl reduced the permeability of soybean roots to water flow. Root L_p dropped from 6.7 to 4.4×10^{-5} cm s^{-1} MPa^{-1}, as Ψ_{soln} was lowered from that of controls by only 0.03 MPa. No significant difference in mean L_p was evident between roots grown at −0.13 and −0.17 MPa, but with further additions of salt, L_p continued to decline. No differences in root L_p were evident with additions of NaCl beyond Ψ_{soln} of −0.20 MPa. Root system L_p of plants grown at a Ψ_{soln} of −0.26 MPa was only 1.9×10^{-5} cm s^{-1} MPa^{-1}, a value more than 70% below that of controls.

L_p was strongly correlated with the RS, with larger values of L_p observed in seedlings with lower RS (Fig. 3). The relationship can be described by an exponential equation of the form $L_p = ae^{bRS} + c$, where parameters a, b, and c are empirical constants.

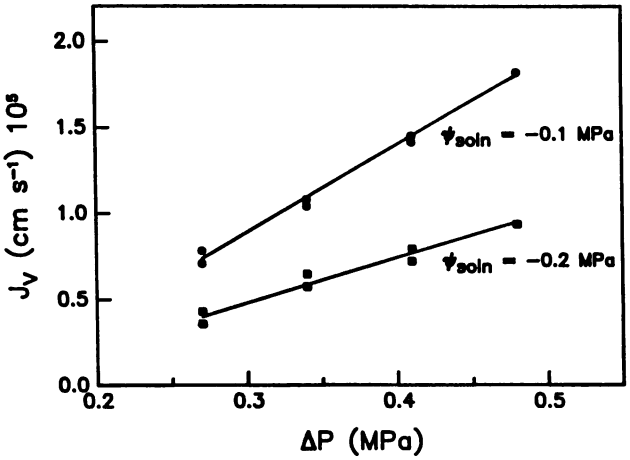

Figure 1. Relation between volume flux of water (J_v) and applied hydrostatic pressure (ΔP) for two representative seedlings, one grown in Hoagland solution ($\Psi_{soln} = -0.10$ MPa) and the other in solution to which NaCl had been added ($\Psi_{soln} = -0.20$ MPa). L_p was estimated for each seedling as the slope of the regression of J_v on ΔP. Four flux determinations were made at each pressure (many data points overlap).

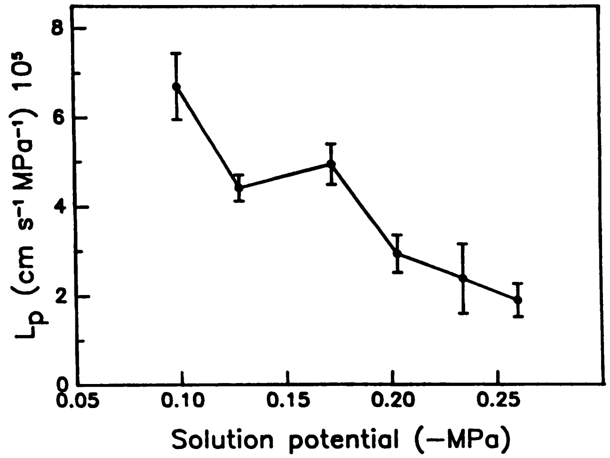

Figure 2. L_p, as influenced by the solution osmotic potential at which seedlings were grown. L_p is expressed on the basis of root surface area. Points are means ± 1 SE (n = 4 or 5).

DISCUSSION

The pressure-flux technique employed in this study yields an average L_p for the entire root surface in contact with solution, and spatial heterogeneity in either local hydraulic conductivity or reflection coefficients within the root system cannot be resolved by this approach. Permeability of these root systems to water probably varied with tissue age and stage of development, with basal portions likely being less conductive than more recently matured portions. Kevekordes *et al.* (6), for example, demonstrated that the potential flow of xylem sap in soybean roots was strongly conditioned by

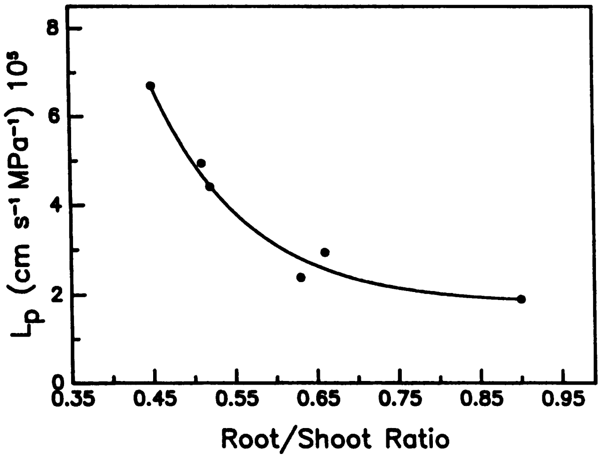

Figure 3. Relation between the *RS* and L_p for soybean seedlings grown in nutrient solutions where the solution potential was varied by additions of NaCl. Points are means of 4 or 5 observations. Regression equation:

$$L_p = 252.47 \cdot [\exp(-8.77 \cdot RS)] + 1.80;\ R^2 = 0.97.$$

the extent of maturation of large metaxylem elements, and Oosterhuis and Wullschleger (12) reported a large increase in water flux through cotton roots at 10 to 12 cm proximal to the root tip, which was associated with secondary xylem development.

The possibility that salinity could have altered the relative proportions of highly conductive and less conductive developmental regions of roots cannot be ruled out. Further, although no obvious visual differences in root branching were evident in salinized *versus* control plants, branching pattern was not specifically quantified. If salinity decreased branching and if, as Passioura (13) has suggested, axial resistance is a significant component of total root resistance, then the computed L_p would underestimate the true value, even if radial resistance remained unchanged.

In light of these uncertainties, the results of this study can be interpreted only in terms of an integrated, whole-root-system response to osmotic stress. Further investigations of salinity effects on root anatomy and morphology and on the heterogeneous nature of root hydraulic conductivity are needed. Any definitive test of salinity effects on water and solute flow in roots will require accurate determinations of L_p, σ, and rates of solute uptake at discrete sites along the root axis.

The values of L_p measured in nonstressed soybean plants are in close agreement with those estimated by Fiscus (2). Further, the decrease in root system L_p observed with increasing salinity of the growth solution (Fig. 2) is consistent with the results of O'Leary (10, 11), where reductions in the osmotic potential of growth solutions by additions of NaCl led to sharply reduced rates of water movement through detopped *Phaseolus vulgaris* seedlings. The drop in soybean root L_p contrasts, however, with the observation by Shalhevet *et al.* (14) that root hydraulic conductivity of intact tomato and sunflower plants was unaffected by Ψ_{soln} in split-root experiments using salinized nutrient solutions. Munns and Passioura (8) observed no change in root hydraulic resistance of intact, NaCl-treated barley plants, a salt-tolerant crop species, but large increases in resistance were induced in the salt-sensitive white lupin.

Average root system permeability to water was reduced to a marked extent as a result of growing in mildly saline solution. Growth in NaCl for 14 d at −0.17 and −0.26 MPa resulted in reduction in L_p from that of controls by 27 and 72%, respectively. This response may have been conditioned by increased suberization of cell walls or by increased deposition of secondary wall materials, as suggested by O'Leary (10). In light of the possibility that these processes may have been modified by Ψ_{soln}, and considering the possible effects of Ψ_{soln} on differentiation of conducting tissue discussed above, it is not possible to conclude from these data that the measured reductions in hydraulic conductivity of the root system have been caused by a decrease in membrane permeability *per se* within the primary absorbing regions of roots.

The strong association between *RS* and L_p (Fig. 3) may reflect the combined effects of salt on the acquisition and allocation of resources among plant organs and on the hydraulic conductivity of roots. Root growth of nonhalophytic plants exposed to saline media has generally been observed to be impaired to a lesser degree than shoot growth (9). The association between *RS* and L_p noted here is consistent with such reports and appears to be a reflection of the differential sensitivity of growth among organs to salinity. Seedlings exposed to high concentrations of NaCl exhibited both increased root/shoot ratio and decreased hydraulic conductivity. Fiscus and Markhart (4) demonstrated that L_p was related in a complex manner to plant age and size for *P. vulgaris* seedlings. They observed that root system size was the dominant factor in controlling water transfer characteristics and concluded that factors associated with slow growth may act to reduce L_p. The data presented here for soybean are consistent with those for *Phaseolus* and suggest that the shifting balance between absorbing and transpiring organs may itself be important in determining root system transport parameters. An alternative hypothesis is that the evaporative surface of the plant is controlled by plant and root conductances.

When a solution bathing plant roots is salinized, the water potential at root epidermal surfaces decreases. The extent to which this drop is transmitted throughout the hydraulic pathway depends on the overall hydraulic conductivity of the plant (C) and the rate of transpiration (E). Assuming that there is no significant storage capacity, the water potential of the leaf (Ψ_{leaf}) is related to the water potential of the solution (Ψ_{soln} by $\Psi_{leaf} = \Psi_{soln} - (E/C)$. Assuming that root membranes are nearly impermeable to solutes, a decrease in Ψ_{soln} due to additions of NaCl would result in an identical drop in Ψ_{leaf} only if E/C was not altered. If (as observed here) salt decreased C, the drop in Ψ_{leaf} must necessarily be larger than the drop in Ψ_{soln}. The result would be a lowered rate of water flux through the pathway, even if the driving gradient is maintained by osmotic adjustment in leaves. Reduced delivery of water to leaves would, in turn, be expected to result in loss of turgor and impairment of leaf expansion.

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