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Salinity and the Hydraulic Conductance of Roots

By

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Abstract

The effect of salinity on hydraulic conductance of intact roots of tomato (*Lycopersicon esculentum* Mill.) and sunflower (*Helianthus annuus* L.) was determined in split-root experiments using salinized nutrient solutions. Experiments were conducted in controlled climate chambers under two or three relative humidity levels and four solution osmotic potential levels.

The relationship between water flux through roots (J_v) and total water potential difference between the leaves and the root medium ($\Delta\psi$) was linear, usually with a small intercept. Thus, the root hydraulic conductance (L) was not affected by salinity within the range of fluxes obtained in these experiments, with $L = 0.036$ mm h^{-1} bar^{-1} for tomato and $L = 0.0167$ mm h^{-1} bar^{-1} for sunflower. Our results agreed with theoretical analysis of coupled water and ion uptake.

From Cl^- and Na^+ uptake data, the reflection coefficient (σ) for tomato roots was calculated as 0.956, which was compatible with the near-zero intercept. A large intercept for sunflower could not be readily explained.

Relative humidity strongly affected root growth, with more rapid growth under low humidity conditions. Transpiration of sunflower plants was reduced by 20% when the relative humidity was increased from 34% to 84%, whereas transpiration in tomato was reduced 50%.

Introduction

The flux of water into plant roots (J_v) is governed by (1) the driving force, the total water potential difference across the root ($\Delta\psi$), and (2) resistance, or inversely, the apparent conductance of water through the root (C). The relationship may be described by the general equation, $J_v = C\Delta\psi$. Contrary to early assumptions in modelling water movement through plants, roots conductance has been shown to increase as flux increases (Slatyer 1967, Kramer 1969). Changing root conductance enables the plant to satisfy transpirational demands without developing undue stress, *i.e.*, steeply lowering its leaf water potential. Barrs (1973) calculated by linear extrapolation that to increase the transpiration rate induced by lowering the atmospheric humidity, tomato leaf water potential would have to drop to −15 bars, instead of the measured −6 bars, if conductance had not increased. For sunflower the adjustment in conductance was even greater. Since the plant's main resistance to liquid water flow is in its roots (Kramer 1969), any changes in root conductance may profoundly affect the plant's water economy.

The salt concentration of the root media is known to affect plant water status, and it might also affect root conductance. Understanding the interrelationship between root conductance and the osmotic potential of the root medium is particularly important for heterogeneous systems, where the osmotic potential of the root medium varies in space and time (Shalhevet and Bernstein 1967). Published results on the effect of osmotic potential on root conductance are conflicting. Brouwer (1953) measured water flux through a single root and found that root conductance increased when a root was exposed to a −2.5 bar sugar solution. However, in root exudation experiments, root conductance of tomato (Mees and Weatherley 1957), corn (Klepper 1967), and bean (O'Leary 1969) decreased as osmotic potential decreased. Arisz *et al.* (1951) found no effect on bean roots. In exudation experiments the nature of the pressure differences is not equivalent to the water potential differences created by the transpiration stream in the whole plant. Consequently, root conductance determined from exudation experiments may not equal the root conductance of a transpiring plant.

Janes (1970), working with whole pepper plants under two light intensities and using polyethylene glycol 400 as an osmoticum, found linear relationships between transpiration and the difference in water potential between leaf and

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nutrient solution. From these linear relationships, we calculated that the hydraulic conductances of the plants were 0.030 and 0.012 mm h^{-1} bar^{-1} under high and low light intensities, respectively, regardless of osmotic potential. Thus, conductance was affected by transpiration flux when the latter was controlled by light intensity, but not when controlled by osmotic potential. Pooling his data and plotting conductance versus transpiration (or J_v), Janes (1970) found a nonlinear relationship. This indicated an apparent increase in root conductance with increasing J_v due to an intercept on the transpiration versus $\Delta\psi$ plot, rather than a gradual, real change in conductance.

Recently, two similar theoretical studies were published by Dalton *et al.* (1975) and Fiscus (1975) who related water uptake to ion uptake. Both studies were based on the theory of coupled flow of solutes and water across semipermeable membranes, as described in detail by Katchalsky and Curren (1965). This theory indicated that nonlinearity between flux and driving force may be due to relative changes in hydraulic and osmotic potential differences.

The objectives of our work were to obtain quantitative information relating water uptake and root conductance to the osmotic concentration of the nutrient solution, using whole plants, and to determine the applicability of a mathematical flow model for the experimental situation. We also made some observations on the effect of relative humidity on plant response.

Abbreviations: J_v, water flux; ψ, total water potential; ψ_O, osmotic potential; ψ_L, leaf water potential; ψ_{O_L}, leaf osmotic potential; P, hydraulic pressure; P^*, total pressure equivalent; π, osmotic pressure; ω, osmotic permeability coefficient; σ, reflection coefficient; C, apparent root conductance; L, root hydraulic conductance; S, selectivity; k, active ion uptake; RH, relative humidity.

Materials and Methods

Three separate experiments were conducted in sunlit climate chambers under controlled temperature and RH (Hoffman and Rawlins 1970). Tomato (*Lycopersicon esculentum* Mill. cv. Heinz 1350) was used in two experiments and sunflower (*Helianthus annuus* L. cv. Russian Mammouth) in the third.

Experiment I (tomato): A split-root technique was employed with salinity treatments applied to a small fraction of the root system. This permitted treatment effects to be restricted to the roots studied, without significantly affecting plant shoots.

On January 13, 1975, seeds were germinated in the dark, between papers supported on stainless steel screens over one-tenth strength nutrient solution. The nutrient solution has the following composition at full strength: 6 m*M* KNO_3, 5 m*M* $Ca(NO_3)_2$, 3 m*M* $MgSO_4$, 0.35 m*M* KH_2PO_4, 100 μM Fe as NaFe diethylene triamine pentaacetate, 46 μM H_3BO_3, 9 μM $MnCl_2$, 0.8 μM $ZnSO_4$, 0.3 μM $CuSO_4$ and 0.1 μM H_2MoO_4. After germination, the top paper was replaced with vermiculite and the seedlings were allowed to develop for 6 days. Uniform-size seedlings were selected and transferred to half-strength nutrient solution in large trays, which were placed in a climate chamber at 50% RH and with gradual daily temperature variations between 30°C in early afternoon and 25°C in early morning. This temperature scheme was used for all the experiments.

When 21 days old, the tomato plants were transplanted into rectangular polyethylene containers (2 plants/container). The root systems were split by separating two upper root branches from each plant into an adjoining identical container, leaving the remaining roots in the other. Each container was filled with 3.5 liters of half-strength nutrient solution, which was continuously stirred and aerated with humidified air. The containers were wrapped with aluminium foil and covered with tight-fitting covers having holes punched for the stems and for water additions. Styrofoam sheets were placed on the covers for plant support. Sixteen pairs of containers were placed in one climate chamber at 35% RH and 16 pairs in a second chamber at 85 to 95% RH. We thus attempted to obtain differences in water uptake by using two humidity levels.

When the plants were 35 days old, the nutrient solution in both containers was renewed and sufficient salt ($CaCl_2$ + NaCl, 1:2 molar ratio) was added to the split-root containers to give three levels of osmotic potential (ψ_O): −1, −2, and −3 bars. One treatment was left with half-strength nutrient solution (−0.4 bar) as a control. All treatments were replicated four times in a randomized complete block design. Data from each chamber were analyzed separately by analysis of variances. Salt was added after sunset, to minimize any possible shock effect of the sudden increase in ψ_O. After 24 h, ψ_O of the main root system was lowered to −1 bar, in an attempt to increase the rate of water uptake from the treated roots, but we observed no effect.

The solution in the split-root containers was replenished continuously with a constant level device (Figure 1), which consisted of an L-shaped capillary tube, pulled on both ends to form a very small diameter air inlet and a somewhat larger diameter air outlet. The tube was connected to the side arm of a glass tee which had one end attached to a closed 100-ml buret and the other extended into the solution. By adjusting the distance between the solution level and the air outlet, any slight change in the solution level (about 0.075 mm or 1.5 ml) resulted in a delivery of an equivalent quantity of distilled water from the buret (±0.3 ml). The distance was controlled by the diameter of the air outlet, while the inlet, diameter and length controlled the sensitivity of the device to solution level changes. Water uptake was measured by buret readings at 10:00 and at 15:00 hours, when solution temperatures were also recorded.

The solution in the main-root containers was replenished to a predetermined level twice daily (at 8:00 and 16:00 hours) using distilled water and a hook gauge.

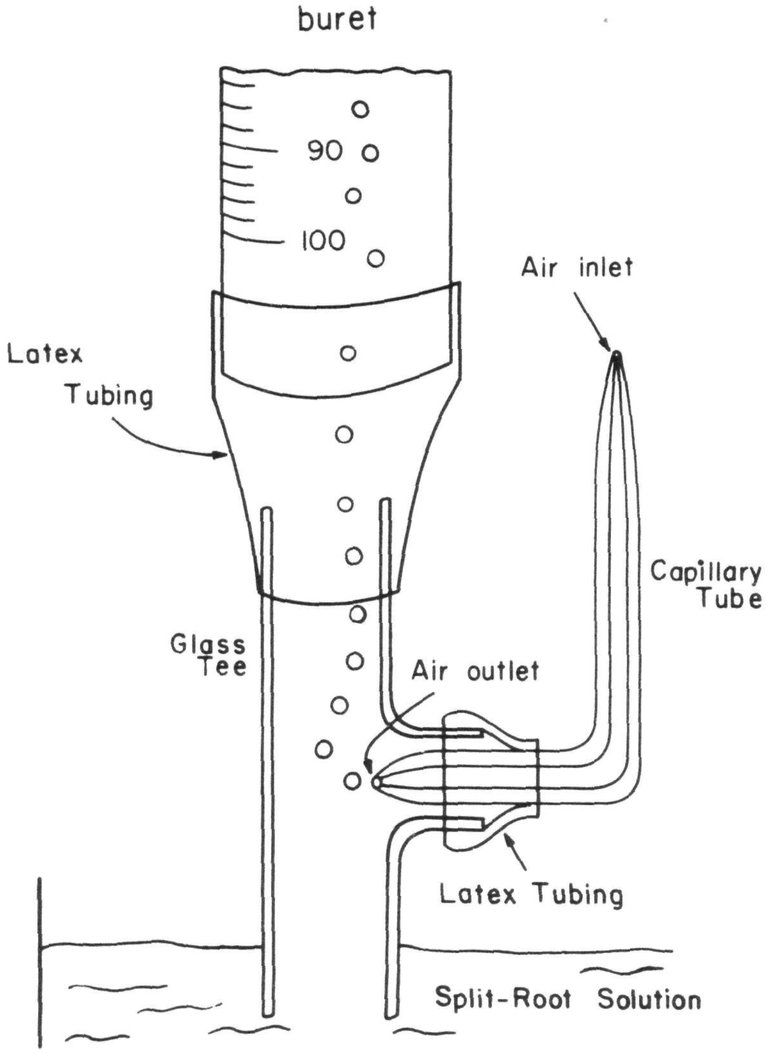

Figure 1. *Schematic of constant-level water device.*

Leaf water and osmotic potentials (ψ_L and ψ_{L_O}) were measured between 13:00 and 13:30 hours, when ψ_L is minimum (Hoffman and Rawlins 1972). On three consecutive days leaf discs (10 mm in diameter) were removed and measured with a Peltier cooled thermocouple psychrometer after equilibrating for about 1.5 hours, as described by Hoffman *et al.* (1971). On the fourth day at 09:00 hours, the plants were harvested. Their leaf area was measured with a leaf area meter (Lambda Instruments, Inc.); and their root fresh weight was measured after rinsing the root and draining in a centrifuge at 65 *g* for 5 min. Plant material was dried at 70°C for chemical analysis of Na^+ and Cl^- using standard procedures (Maas and Ogata 1972).

Experiment II (tomato): In the second experiment the whole, rather than just a part of the root system, was bathed in salt solutions. The initial procedure was similar to experiment I, except that when the plants were 23 days old, they were transferred to three climate chambers under three RHs: high (87%), medium (52%) and low (32%). Salinity treatments were applied 2 days later at 20:00 hours by replacing the half-strength nutrient solution with a salt solution (NaCl + $CaCl_2$) to achieve treatments having −1, −2, or −3 bars osmotic potential. Each salinity treatment was replicated three times in each chamber with 8 plants per 14-liter container. Transpiration was determined by weight loss during a 5-h period (09:30 to 14:30). Just before measurements were started, plants in one container of each treatment were harvested and analyzed to determine salt uptake. The experiment was continued for 2 days after which plants were harvested as described above.

Experiment III (sunflower): Experiment III was conducted concurrently with experiment II using the split-root technique described in experiment I. After germination, plants were grown for 22 days in half-strength nutrient solution in a growth chamber artificially lighted with fluorescent and incandescent lamps having an average spectral intensity in the visible range of 58 W/m^2 at plant height. The temperature was maintained at 25°C and RH was uncontrolled. The plants were then transferred to the sunlit climate chamber at 53% RH and their root systems were split, as described above. After sundown 5 days later, the split parts of the root systems were salinated as in experiment I to obtain osmotic potentials of −1, −2, −3 or −4 bars. Each salinity treatment was replicated four times. At this time the nutrient solutions of the main root systems were renewed with fresh half-strength solution. Two pots were harvested when the salinity treatments were initiated, and two pots remained with nutrient solution as controls.

The procedure described for experiment I was repeated, except that at 16:00 hours daily the RH in the chamber was changed from 53 ± 3% during the first day to 84 ± 9% during the second day and to 47 ± 5% during the last day. The solution in the main root containers was replenished thrice daily (08:00, 12:00 and 16:00 hours). Leaf area was calculated for the first day from the product of measured leaf width, length and a coefficient of 0.707. The coefficient was calculated from measurements of leaf width, length and area determined at the end of the experiment. The plants were harvested and analyzed by the same procedure as in experiment I.

Daily (between 13:00 and 13:30 hours) leaf water potentials were measured psychrometrically and with a pressure chamber on detached leaves of relatively uniform age.

Results and Discussion

(a) *Relative humidity, growth and leaf water potential*

Exposure to salinity of 26 to 34% by weight of the total root system of tomato and 23% of that of sunflower had no measurable effect (Tables 1, 2, 3) on transpiration rate, leaf area and weight, or leaf water potential (ψ_L). The only measurable effect was on water and ion uptake from the salinized portion of the roots. In experiment II, where the whole root system was exposed to salinity, both water uptake and transpiration were influenced. Transpiration was decreased by 18% (from 177 to 145 ml h^{-1} m^{-2}) by decreasing osmotic potential from −1 to −3 bars. During the second day of the experiment, transpiration decreased 23% more under low RH than under high RH, indicating partial stomatal closure in response to high evaporative demand.

Table 1. *Root water uptake, transpiration rate, leaf area and root fresh weight of tomato plants under split root conditions as a function of osmotic potential of nutrient solution at two relative humidities* (Expt. I). * significant at 5%, ns = not significant, SE = standard error.

					Split root		
RH %	Osmotic potential bar	Water uptake main root ml h^{-1} g^{-1}	Transpiration ml h^{-1} m^{-2}	Leaf area m^2	Fresh weight g	Dry matter %	Main root fresh wt. g
34							
	−0.2	1.70	287	0.313	17.5	5.0	38.2
	−1.1	1.54	280	0.318	23.4	4.4	42.6
	−1.9	1.67	252	0.322	22.9	4.3	40.8
	−2.6	1.87	273	0.342	20.1	4.3	39.4
	mean	1.70	273	0.324	21.0	4.5	40.2
	SE	0.10 ns	11 ns		2.0 ns		2.0 ns
84							
	−0.2	1.05	184	0.287	11.5	3.8	29.6
	−1.1	1.12	179	0.296	14.0	3.4	33.2
	−1.9	1.31	189	0.296	9.5	3.8	32.8
	−2.7	1.13	156	0.286	11.8	3.5	38.2
	mean	1.15	177	0.291	11.7	3.6	33.4
	SE	0.07 ns	11 ns		2.2 ns		1.8*
	Low/high ratios	1.48	1.54	1.11	1.80	1.24	1.20

Mean ψ_L, on the other hand did not respond to RH.

The results show that the split-root technique was suitable for studying the response of the apparent hydraulic conductance to environmental factors while the roots were still part of an actively transpiring plant. The split-root method has an advantage over the excised-root technique, where pressure differences are either artificially induced by applying outside pressure or are osmotic. Most likely, flow will be influenced by the nature of the pressure difference as reported by Mees and Weatherley (1957). Differences produced by leaf suction will not have the same effect as artificially produced pressure differences. This will be discussed in more detail when dealing with coupled water-ion uptake.

Relative humidity had a strong effect on tomato root development rate but less on top growth, especially with the treated roots, where the root fresh weight was almost doubled under low, as compared with high, ambient RH. The differential root development resulted in a very small difference in water uptake (13% between the RH treatments, see Figure 2), as compared with a 50% difference in uptake by the main root system (Table 1). Apparently, at least on the short-term basis, root growth responded to the evapora-

Table 2. *Root water uptake, transpiration rate, leaf area and root fresh weight of sunflower plants under split-root conditions as a function of osmotic potential of nutrient solution* (ψ_O) *at two relative humidities* (Expt. III). * significant at 5%, ns = not significant, SE = standard error.

	Water uptake main root ml h^{-1} g^{-1}		Transpiration ml h^{-1} m^{-2}			Split root		
ψ_O bar	Low RH	High RH	Low RH	High RH	Leaf area m^2	Fresh weight g	Dry matter %	Main root fresh weight g
−0.2	1.03	0.89				43.2	3.5	127
−0.8	1.05	0.92	538	433	0.333	45.0	3.5	133
−1.7	1.20	1.14	470	398	0.356	41.0	3.4	115
−2.6	1.04	0.91	459	382	0.348	33.6	3.4	138
−3.5	1.17	1.03	471	412	0.348	38.2	3.7	128
mean	1.10	0.97	485	406	0.346	39.4	3.5	128
SE	0.04*		16*	15 ns	0.010 ns	7.7 ns		4.2*

Table 3. *Total* (ψ_L), *osmotic* (ψ_{O_L}) *and turgor* (ψ_{P_L}) *leaf water potentials for tomato and sunflower as a function of osmotic potential of nutrient solution* (ψ_O) *at 2 relative humidities* (Expt. I and III). SE = Standard error of overall RH mean for tomato, and salinity treatment mean for sunflower, ns = not significant.

		34% RH			84% RH		
Species	Osmotic potential bar	Leaf water potential bar	Leaf osmotic potential bar	Leaf turgor potential bar	Leaf water potential bar	Leaf osmotic potential bar	Leaf turgor potential bar
Tomato							
	−0.2	−4.7	−11.5	6.8	−4.9	−9.6	4.7
	−1.1	−4.3	−11.5	7.2	−4.1	−9.6	5.5
	−1.9	−4.5	−10.5	6.3	−4.9	−9.6	4.7
	−2.6	−4.7	−11.5	6.6	−4.2	−9.4	5.2
	mean	−4.5	−11.2	6.7	−4.6	−9.6	5.0
	SE	0.25	0.22		0.39	0.33	
Sunflower							
	−0.8	−5.2	−8.8	3.6	−3.4	−7.7	4.3
	−1.7	−5.3	−8.6	3.3	−3.6	−7.9	4.3
	−2.6	−4.5	−8.1	3.6	−3.4	−7.0	3.6
	−3.5	−4.0	−7.2	3.2	−3.5	−7.4	3.9
	mean	−4.8	−8.2	3.4	−3.5	−7.5	4.0
	SE	0.63 ns	0.60 ns		0.38 ns	0.31 ns	

tion demand of the atmosphere. When the demand was high, root growth increased. The main part of the root system, as well as plant tops, was fairly well-developed when placed under different RH and therefore showed smaller growth differences in response to RH than the split roots.

The triggering mechanism for root response to ambient RH is not clear. Difference in leaf turgor potential is one possibility; plants exposed to low RH had higher turgor than those exposed to high RH (6.7 vs. 5.0 bars, respectively; Table 3). Also, the dry matter content of the treated roots at low RH was higher (4.5 vs. 3.6%; Table 1).

Sunflower plants responded somewhat differently. Comparing the two plants on the same basis is not possible, because of differences in experimental technique. Nevertheless, the plants under humid conditions seemed more turgid (4.0 vs. 3.4 bars; Table 3). Furthermore, the leaf-to-root ratio of sunflower (1.8 g/g) was almost three times smaller than that of tomato (5.6 and 4.2 g/g for the high and low RH, respectively). Evidently, sunflower requires a much larger root system than tomato to supply water and nutrients for an equivalent leaf yield.

Another difference in sunflower and tomato behavior is the control of transpiration. Although RH changed rapidly in the sunflower experiment to avoid root growth adjustment to RH, the difference in transpiration between the high and low RH was only 20%, whereas the difference was 50% with tomatoes. Tomato showed no differences in ψ_L between the two humidities, while sunflower plants had over 1 bar higher ψ_L under high as compared with low RH (−3.5 vs. −4.8 bars). The reasons for these differences seem to result from differences in transpiration control mechanisms. While tomato regulated transpiration through stomatal movement, sunflower with stomates less responsive to humidity under (Whiteman and Koller 1967), reduced ψ_L in response to a decrease in RH.

Our psychrometric ψ_L values were used to relate with $\Delta\psi$. The pressure chamber ψ_L of sunflower was consistently lower than that measured psychrometrically as found by Kaufman (1968). For example, under low RH the psychrometric mean value was −4.8 bars as compared with −6.4 bars for the pressure chamber. Under high RH, the respective values were −3.5 and −7.0 bars.

There are systematic errors inherent in the pressure chamber method which will result in low ψ . High xylem osmotic potential (Boyer 1969), the filling of air spaces in the leaf during pressure buildup (Oertli *et al.* 1975) or high leaf temperatures may be only some of the sources of error. Consequently, although the pressure chamber may be useful under field conditions, where relatively low ψ_L values are common, under controlled conditions it may be too crude a tool.

The osmotic potentials of both tomato and sunflower leaves were higher under high than under low RH, but they were not significantly affected by the ψ_O (Table 3).

(b) *Root hydraulic conductance*

Figure 2 shows the linear relationship of the flux through the roots to the total water potential difference between the root substrate and the leaves for both tomato and sunflower. Table 4 gives the coefficients describing the linear lines. These results are compatible with the theoretical treatment given by Dalton *et al.* (1975) and Fiscus (1975). Dalton *et al.* (1975) combined equations describing water flux and solute flux to obtain

$$J_v = L(\Delta P - \sigma S \pi_0) \tag{1}$$

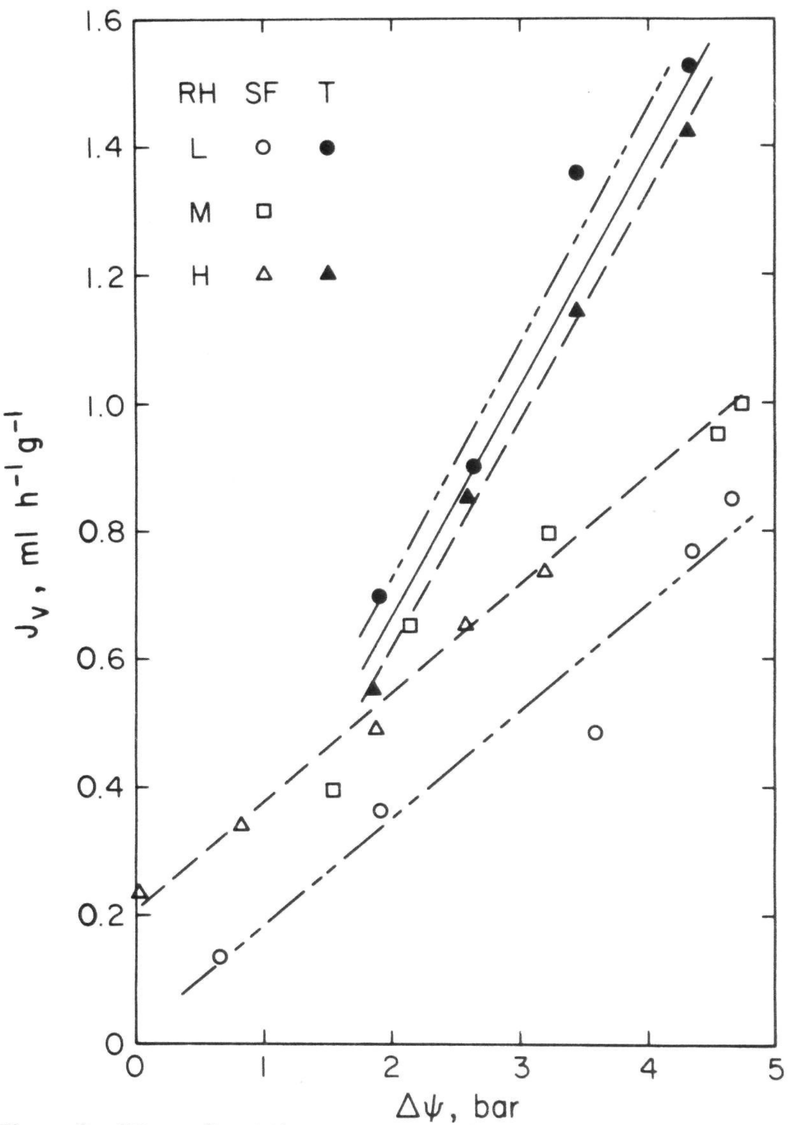

Figure 2. *Water flux* (J_v) *into tomato* (T) *and sunflower* (SF) *roots as a function of the water potential difference* ($\Delta\psi$) *from the root medium to leaf at different relative humidities* (L = low, M = medium, H = high).

where L is a hydraulic conductance of the roots (not to be confused with flux-dependent apparent conductance, C); ΔP is the hydraulic pressure difference across the membrane; σ is the reflection coefficient; and π_0 is the osmotic pressure of the ambient solution. Subscripts 0 and i designate ambient and xylem solutions, respectively. S describes membrane selectivity and is defined as

$$S = \frac{\sigma - nRTk/(\pi_0 J_v)}{1 + nRT\omega/J_v} \qquad (2)$$

where n is the sum of the cation valences of the completely dissociated salt; R is the gas constant; and T the absolute temperature; ω is the osmotic permeability coefficient for ion diffusion through membranes; and k is the active ion uptake component.

Table 4. *Linear coefficients for* J_v *vs.* $\Delta\psi$ *of Figure 2.*

Species	Relative humidity	Intercept ml h⁻¹ g⁻¹	Slope ml h⁻¹ g⁻¹ bar⁻¹	r^2
Tomato				
	High	−0.084	0.352	0.997
	Low	−0.002	0.361	0.965
	High + low	−0.045	0.360	0.947
Sunflower				
	High + medium	0.210	0.168	0.966
	Low	0.017	0.167	0.933

The correspondence between the theory and the experimental results can be seen by replacing the sum of the hydraulic and negative osmotic pressure component differences with the total pressure equivalent difference ($\Delta P^* = \Delta P - \Delta\pi$). The total pressure equivalent (P^*) is equal to the negative of total water potential (ψ), when the osmotic component is corrected for the partial specific volume of water. Introducing ΔP^* and $\Delta\pi = S\pi_0$ into Equation (1) results in

$$J_v = L\Delta P^* + (1 - \sigma)SL\pi \qquad (3)$$

At large flux rates, S approaches σ and Equation (3) reduces

$$J_v = L\Delta P^* + (1 - \sigma)\sigma L\pi_0 \qquad (4)$$

From Equation (4), a plot of J_v versus ΔP^* results in a linear line of slope L and intercept $(1 - \sigma)\sigma L\pi_0$, from which we can estimate the value of σ. As σ approaches unity (Dalton *et al.* 1975), the intercept approaches zero and π_0 (or ψ_O) will have a relatively small effect on J_v, as is obvious from Equation (4).

The slope of the lines in Figure 2 may appropriately be considered as the hydraulic conductance (L) of the roots. Thus, for tomato, L was 0.360 ml h^{-1} g^{-1} bar^{-1}, while for sunflower it was half as large, 0.167 ml h^{-1} g^{-1} bar^{-1}. There was no apparent effect of ψ_O on root resistance to water entry within the range employed in these experiments. Except for sunflower at high and medium RH, the intercept of the lines was very near zero, as predicted by the theory. Possible reasons for the high intercept for sunflower at high RH is discussed later.

We estimated root diameter by measuring randomly selected samples of roots (or a photographic print for sunflower) using a cathetometer. The mean diameter for both tomato and sunflower was found to be about 0.4 mm. As root density is approximately 1 g cm^{-3}, root weight was converted to root area by multiplying by 10^4 mm^2 g^{-1}. The value of L on a root area basis is about the same as those typically reported in the literature (Kramer 1969, Slatyer 1967) for single roots as determined with potometers.

Because of technical difficulties in experiment II, we could not measure ψ_L for each treatment separately. Therefore, our results showing J_v vs. $\Delta\psi$ are not reported here. Treatment effects on ψ_L precluded using a mean ψ_L for each RH to compute $\Delta\psi$ for each treatment, as we did in experiment I. In the sunflower experiment, enough samples were obtained for psychrometric analysis, to allow $\Delta\psi$ to be computed for each treatment independently.

The relationship between J_v and either ΔP or ΔP^* from Equations (1) and (3) for tomato roots at two levels of

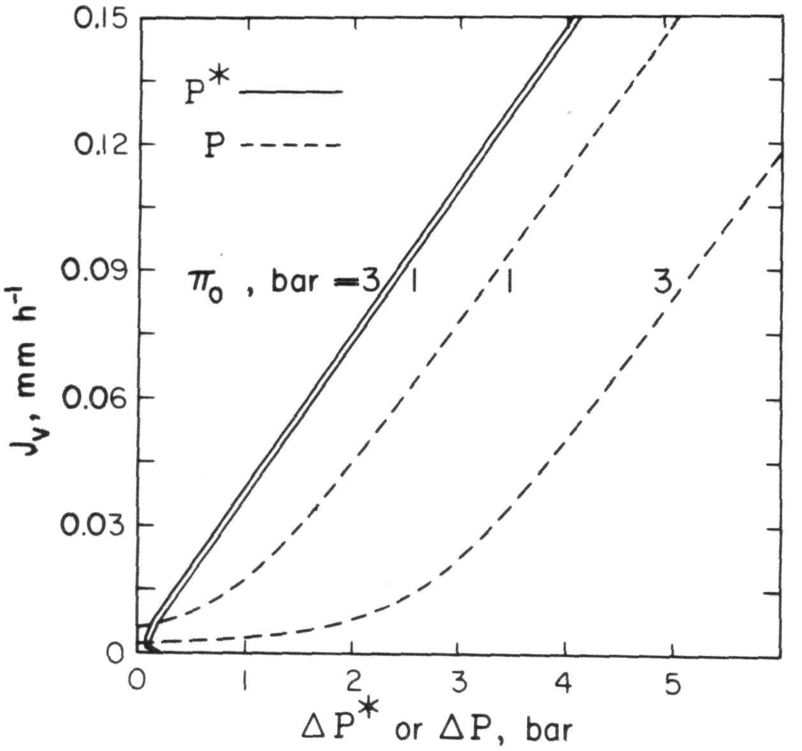

Figure 3. *Water flux* (*J*) *into tomato roots at 1 and 3 bars osmotic potential of the nutrient solution* (π_0) *as a function of the total pressure equivalent difference* (ΔP^*) *and the hydraulic pressure difference* (ΔP), *based on theoretical relationships* (equations 1 and 3). $L = 0.036$ mm h^{-1} bar^{-1}, $\sigma = 0.966$, $\omega = 0.02$ meq m^{-2} h^{-1} bar^{-1}, $k = 0.14$ meq m^{-2} h^{-1}, n = 2.

osmotic pressure of the nutrient solution (π_0) is given in Figure 3. The values for k (0.14 meq m^{-2} h^{-1} for chloride uptake and 0 for Na) and ω (0.02 meq m^{-2} h^{-1} bar^{-1}) were taken from Maas and Ogata (1972) and σ was calculated from our ion uptake data (Table 5) using an equation given by Dalton *et al.* (1975). The value of L (0.036 mm h^{-1} bar^{-1}) was taken from Table 4 and converted to root area. The reflection coefficients for tomato and sunflower are given in Table 5 along with the calculations based on chloride uptake. Similar calculations were made for Na uptake except k was assumed to be negligible. Ion flux was determined by dividing the total ion uptake by the estimated root area and the duration of the uptake. We assumed no diurnal fluctuations in ion uptake. In experiment II, ion uptake rate during the first night after salt was added was the same as the average rate for the 48-hour experimental period (7.1 × 10^{-3} vs. 6.1 × 10^{-3} meq h^{-1} g^{-1}, respectively). Similar results were reported for cotton by Parsons and Kramer (1974) and for bean by Meiri *et al.* (1970). Ion concentration in the xylem solution was calculated from the ratio of ion flux to water flux.

Figure 3 shows that the theoretical relationship of J_v to ΔP^* is indeed linear down to about a 5 × 10^{-3} mm h^{-1} flux, at which there is a reversal in gradient ($\Delta\pi = 0$). Then flow continues to decrease while the total pressure difference actually increases. We observed very small differences in the relationship between J_v and ΔP^* between the two values of π_0 in our calculations. Such small differences would be very difficult to detect experimentally. Also, flow velocities, small enough to observe the reversal in gradient ("negative resistance" in the terminology of Fiscus 1975), are difficult to obtain in an experiment with transpiring plants, and would generally be unimportant, except possibly under conditions of transpiration in the dark.

The relationship of the hydraulic pressure difference to flux is also given in Figure 3, where the relationship is indeed curvilinear with apparent conductance decreasing as J_v decreased. This phenomenon was discussed in detail by Dalton *et al.* (1975) and Fiscus (1975), and underscores the importance of considering the nature of the gradient when studying root resistance.

The intercept in Figure 2 for sunflower at medium and high relative humidities may now be qualitatively examined. The higher intercept indicates a substantial root pressure, causing a flux at zero total pressure difference. Using Equation (4) for $\Delta P^* = 0$, this pressure was calculated as about 7.5 bars or π_i = 8.5 to 10.5 bars. Such high values for the osmotic pressure of the xylem fluid did not seem reasonable

Table 5. *Chloride uptake per plant, ion flux, computed ion concentration in the xylem solution and reflection coefficient* (σ) *from* Cl$^-$ *and* Na$^+$ *uptake as a function of relative humidity and Cl concentration in the nutrient solution.*

Species and RH	Ambient Cl conc. meq l^{-1}	Cl uptake meq/plant	Ion flux meq h^{-1} m^{-2}	Xylem conc. meq l^{-1}	σ_{Cl}	σ_{Na}
Tomato						
34%	26	5.7	0.27	20	0.969	0.973
	79	7.7	0.42	61	0.948	0.941
	mean[1]				0.961	0.959
Tomato						
84%	26	3.0	0.24	21	0.973	0.965
	74	3.6	0.34	62	0.956	0.949
	mean[1]				0.971	0.960
Sunflower						
Avg. of 3 RHs	19	5.5	0.27	34	0.827	0.900
	63	7.9	0.58	115	0.818	0.892
	mean[1]				0.814	0.877

[1] Mean of all treatments.

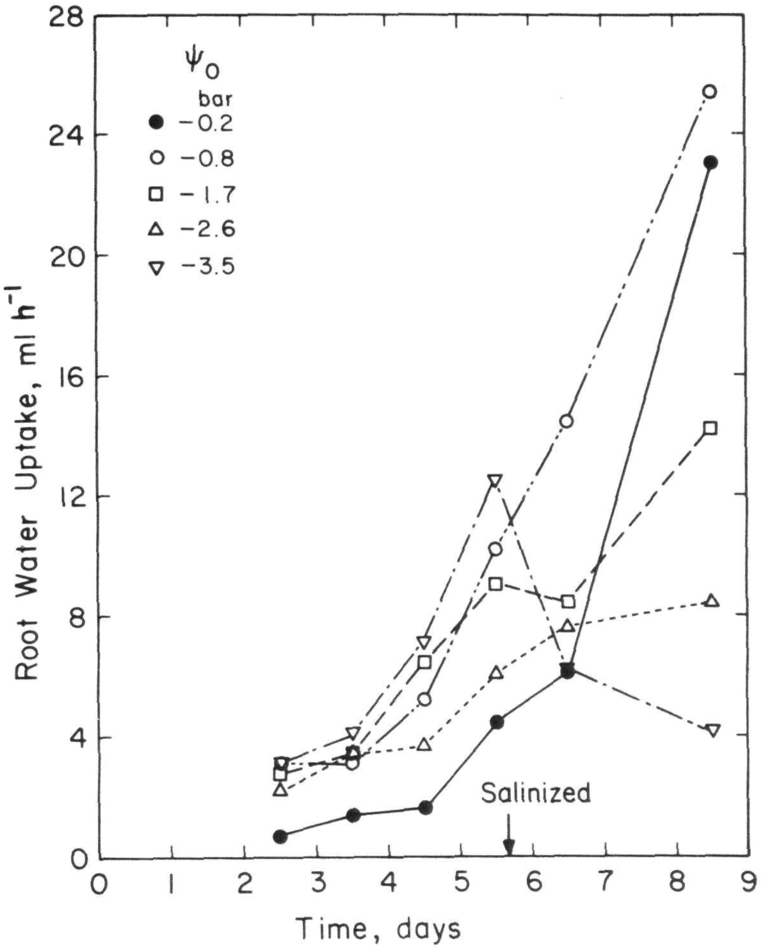

Figure 4. *The time course of water uptake by sunflower plants after root systems were split* (time zero) *at five nutrient solution osmotic potentials* (ψ_O).

on the basis of the rates of ion uptake we found in this experiment (Table 5). The relatively low value of σ (0.845 mean of σ_{Cl} and σ_{Na}) found for sunflower as compared with tomato (0.965) still is far too high to explain the high intercept. Since the RH treatments for sunflower were applied in series on the same plants, (RH was medium the first day and low the last day), they may have been confounded with time effects.

The estimates of sunflower root development may be a source of error. Unlike the tomato experiment, where separated roots were allowed to develop for 2 weeks before salinity treatments were applied, the root systems of sunflower were exposed to salinity only 3 days after they were split. Then the rate of root growth, as indicated by the rate of increase in water uptake in the nonsalinized treatments, was still very rapid (Figure 4). Consequently, root weights in the intervening days were estimated by logarithmic interpolation between final root weights and estimated initial weights. Initial root weights for each treatment were estimated using an initial water flux value of 1 ml h^{-1} g^{-1} of the initially harvested control plants. This rate was similar to the uptake rates of the untreated main part of the root systems (Table 2). If root growth was linear rather than logarithmic, at least for the more saline treatments, the calculated water uptake rates are too high.

Another source of error which may result in a high intercept, is the effect of temperature on ψ_L measurements. During the high RH period, the ambient temperature of the chamber was 3°C higher than during the low RH period and 7°C higher than the psychrometer bath temperature. This may cause a positive potential correction of 1 bar (Hoffman and Rawlins 1972) which would shift the high RH line to coincide with the low RH line (Figure 2).

Whatever the cause for the high intercept, the values of ψ_L computed for tomato were high (Table 4), and the differences between the two RH's were small. These are compatible with the almost zero intercepts and the small differences between the two RH lines in Figure 2.

Apparently, therefore, with normal daytime transpiration, the short-term salinity effect on water uptake only reduces total pressure differences, and/or reduces leaf hydraulic conductance (stomatal closure). Different plant species might have responded differently, like tomato and sunflower in response to RH in this experiment. The long term effect, however, is reduced water uptake from reduced growth.

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