499 AGRO

499

Journal of Agricultural Science, Cambridge (1997), **128**, 439–444. © 1997 *Cambridge University Press*

Effects of salinity on growth, shoot water relations and root hydraulic conductivity in tomato plants

P. RODRIGUEZ[1], J. DELL'AMICO[1], D. MORALES[1], M. J. SÁNCHEZ BLANCO[2]
AND J. J. ALARCÓN[2]*

[1] *Instituto Nacional de Ciencias Agrícolas (INCA), San José de las Lajas, Gaveta Postal 1,*
32700 La Habana, Cuba
[2] *Departamento Riego y Salinidad, Centro de Edafología y Biología Aplicada del Segura (CSIC),*
PO Box 4195, E-30080 Murcia, Spain

(*Revised MS received 10 September 1996*)

SUMMARY

Growth, shoot water relations and root hydraulic conductivity were studied in tomato plants (*Lycopersicon esculentum* cv. INCA9) subjected to different salt concentrations in the root medium. Two experiments were carried out at Instituto Nacional de Ciencias Agrícolas (INCA), Cuba, during May and June 1995. In the first experiment, plants were grown for 13 days in a nutrient solution with 0 or 100 mM NaCl. In the second experiment, the hydraulic conductivity was measured on roots submerged in nine different concentrations of NaCl up to 200 mM. The effect of temperature treatments between 0 and 50 °C on root hydraulic conductivity was also examined. Shoot growth, leaf water potential, leaf stomatal conductance, leaf relative water content and root hydraulic conductivity values decreased more rapidly in the treated plants than in control plants. A strong correlation was found between the root hydraulic conductivity and leaf water parameters, indicating that water flow through the roots was the main factor controlling shoot water relations.

INTRODUCTION

Salinity constitutes the most severe agricultural problem in many parts of the world (Ramage 1980). For this reason, plant response to salinity is one of the most widely researched subjects in plant physiology. However, the main physiological mechanisms of the response to salinity are still unclear. This is because the response to salinity is generally evaluated by using plant growth, ion balance and osmotic adjustment. The water relations of the plant, however, are rarely used. A number of researchers (Sánchez-Blanco *et al.* 1991; Alarcón *et al.* 1993, 1994) have studied the water relations and the osmotic and elastic adjustment capacity of different tomato genotypes under saline stress, and have shown that the growth of salt-treated tomato plants is often limited by the ability of the root to extract water from the soil and transport it to the shoot.

The quantity of water moving from the root to the shoot and its speed determine the quantity and concentration of substances arriving at the shoot (Markhart & Smit 1990). Understanding the forces and resistances that control the movement of water through the soil–plant system is essential in order to understand the influence of salinity on root function and root integration with the shoot.

On the other hand, there is evidence from recent years that leaf expansion can be reduced by low water potential in the growth medium because of chemical signals arising from the roots. In relation to this evidence, the simple inference that changes in shoot water status imply a reduction in leaf growth is not valid (Termaat *et al.* 1985; Davies & Zhang 1991). However, the mechanisms by which salt reduces leaf area expansion need to be investigated, because other authors have observed that the plant water situation under saline stress is an important factor in the control of leaf growth (Neumann *et al.* 1988).

The purpose of the present study was to deepen our understanding of the resistances that limit water flux through the root under saline stress and also to discuss the nature of the signals that may be sent from the root to the shoot in salt-stressed plants. For this purpose, we used tomato, one of the most important and widespread crops in the world, which is moderately salt tolerant.

---

* To whom correspondence should be addressed.

MATERIALS AND METHODS

Plant material and treatments

The experiments were conducted on tomato plants (*Lycopersicon esculentum* cv. INCA9) during May and June 1995. Tomato seeds were germinated and grown in trays of washed silica sand in a growth chamber. Environmental conditions during the germination period were dark, 29 °C and 80% RH. During plant development there was a 12 h photoperiod with a photon fluence density of 80–250 μmol m^{-2} s^{-1} (PAR). Temperature and relative humidity were 29/20 °C and 60/70% during light/dark periods, respectively. Plants were watered daily with deionized water until the first true leaf had developed. During the remainder of the experiment, a nutrient solution was used (Verdure 1981).

In the first experiment, salt treatments were applied 13 days after germination using nutrient solution with 0 and 100 mM NaCl. The saline treatment was maintained over 13 days. Growth, morphological parameters, leaf water relations and root hydraulic conductivity (L_v) were measured during the experimental period. The design of the experiment was randomized with three replicates of ten plants per treatment.

In the second experiment, one additional assay was made in order to discover the effect of salinity and root medium temperature on root hydraulic conductivity. In this instance, the plants were harvested 17 days after germination and the root hydraulic conductivity was measured under different temperature and saline regimes. The salt concentrations used were 0, 25, 50, 75, 100, 125, 150, 175 and 200 mM NaCl at 25 °C, and the temperature treatments were 0, 5, 10, 15, 20, 25, 30, 35, 40, 45 and 50 °C at 25 mM NaCl. A set of 160 plants was used in this experiment (eight plants per temperature and salt concentration).

Measurements of growth and water status

At the end of the first experiment, six plants per treatment (two per replicate) were harvested and root, stem and leaf dry weight measurements were taken. The shoot:root ratio was estimated.

Every 3 days during the salinization period (3, 6, 9 and 13 days after the beginning of the treatments), leaf water potential (ψ_h), leaf relative water content (RWC) and leaf stomatal conductance (g_l) were measured on six plants per treatment. Root hydraulic conductivity was also measured in these plants, but only on days 3 and 9. Leaf water potential was estimated at minimum PAR level using a pressure chamber (Soil Moisture Equipment Co, Santa Barbara, CA, USA) according to Scholander *et al.* (1965). Leaf stomatal conductance was measured at maximum radiation using a DELTA-T DEVICES-MK3 porometer.

Measurements of root hydraulic conductivity

In the first experiment, the root hydraulic conductivity was measured according to Ramos & Kaufmann (1979). The stem was cut with a razor blade 3 cm above the soil surface and the soil was carefully washed away from the roots. Then the root system was submerged in a container of water and placed in the pressure chamber with the cut stump exposed to the outside for 30 min. After a good seal was obtained, the air pressure was increased at an approximate rate of 4 bar/min up to a final pressure of 8 bar. A small piece of plastic tubing was fitted to the stump, and every 3 min the exudate was collected and its volume measured. After the exudation measurements, the root length was estimated using the line intersect method (Tennant 1975). The hydraulic root conductivity was calculated using the formula:

$$C = J/(P \times L)$$

where C is expressed in mg m^{-1} s^{-1} MPa^{-1}, P is the applied hydrostatic pressure in MPa, L is the root length in m and J is the water flow rate through the entire root system in mg s^{-1}.

In the second experiment, the technique for measuring root hydraulic conductivity was the same, but different salt concentrations and root temperatures were applied in a random order to each root system using water (inside the pressure chamber, bathing the roots) at the desired temperatures and NaCl concentrations each time. The temperature of the root medium was kept close to the value required by circulating cold or hot water through tubing coiled around the chamber body.

RESULTS

There were no significant changes in leaf water potentials of control plants during the period 3–13 days after salinity treatment. Salinity induced a rapid decrease in ψ_h from the beginning of the experiment, and remained relatively stable, at *c.* −0·8 MPa over the experimental period (−0·50 MPa lower than those of control plants) (Fig. 1*a*). Differences between treatments were found in leaf stomatal conductance (Fig. 1*b*) and relative water content (Fig. 1*c*). RWC and g_l values in treated plants decreased rapidly compared to the control plants.

The root hydraulic conductivity values decreased in the treated plants (Fig. 2). From day 3 of stress, L_v presented a reduction of *c.* 50% with respect to the control. This reduction was slightly greater after 9 days of stress.

Figure 3 presents the relationships found throughout the experimental period between root hydraulic conductivity (L_v) *v.* g_l and ψ_h. Our data show a significant correlation between changes in L_v and leaf water parameter variations (g_l and ψ_h). The increases

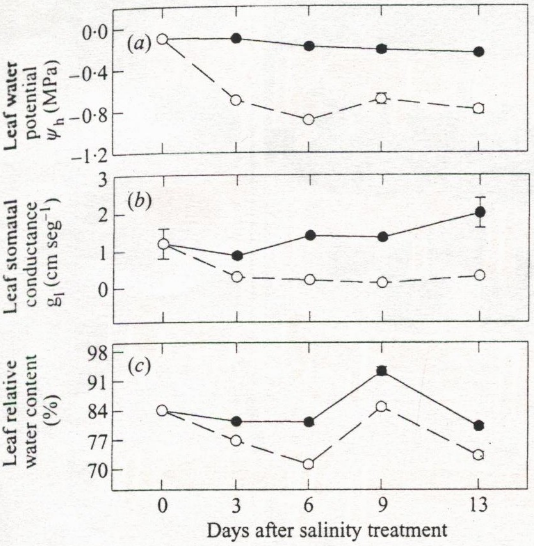

Fig. 1. (*a*) Leaf water potential (ψ_h, MPa), (*b*) leaf stomatal conductance (g_l, cm seg^{-1}) and (*c*) leaf relative water content (%) for tomato (*Lycopersicon esculentum*) in control (●) and saline (○, 100 mM NaCl) treatments during the experimental period. Each point is the mean of six measurements. Vertical bars represent S.E. of the mean (not shown when smaller than the symbols).

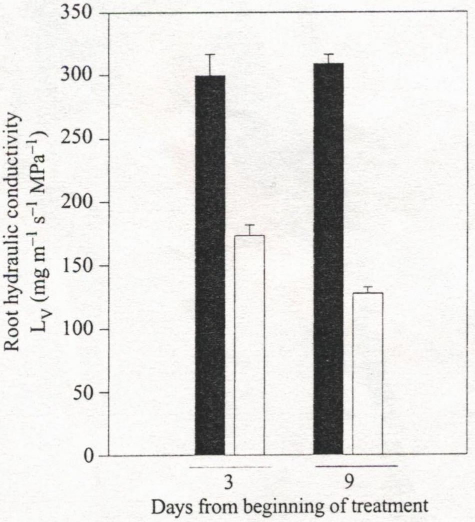

Fig. 2. Root hydraulic conductivity (L_v) for tomato (*Lycopersicon esculentum*) in control (■) and saline (□) treatments, 3 and 9 days from the beginning of the treatments. Each histogram is the mean of six measurements. Vertical bars represent S.E. of the mean.

in L_v values were associated with the highest ψ_h and g_l levels.

At the end of the salinization period, salinity induced a clear reduction in stem, leaf and root dry weight values (Table 1). However, the shoot:root ratio increased significantly in salt-treated plants, indicating that root development was affected more than shoot growth.

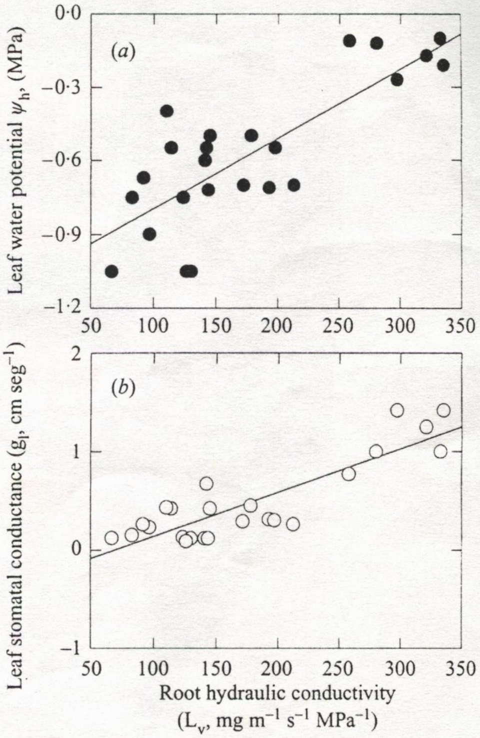

Fig. 3 (*a*) Relationship between root hydraulic conductivity (L_v) *v.* leaf water potential (ψ_h) (●, $y = 0{\cdot}00285x - 1{\cdot}0797$, $r = 0{\cdot}80$) and (*b*) root hydraulic conductivity (L_v) *v.* leaf stomatal conductance (g_l) (○, $y = 0{\cdot}00461x - 0{\cdot}3072$, $r = 0{\cdot}87$). The data were obtained on tomato plants growing under saline and control conditions at different times during the experimental period. Each point was obtained from one individual plant.

The influence of root medium temperature on root hydraulic conductivity is summarized in Fig. 4. The results obtained in this assay showed a strong temperature effect on root hydraulic conductivity.

The effects of different saline treatments, applied during the second experiment, on root hydraulic conductivity, which were measured under standard temperature conditions (25 °C), are shown in Fig. 5. There was no overall linear correlation between the changes in L_v and the concentration of salts in the radicular medium. Two different phases can, however, be observed in this relationship. In the first phase, which occurs at NaCl concentrations of < 50 mM, increases in NaCl are associated with rapid decreases in L_v. In the second phase, a slower rate of L_v decrease was noted for NaCl concentrations > 50 mM.

Table 1. *Leaf, stem, root dry weights (DW, g plant^{-1}) and shoot:root ratio for tomato* (Lycopersicon esculentum) *in control (0 mM NaCl) and saline (100 mM NaCl) treatments at the end of the experimental period*

Treatment (NaCl)	Leaf DW	Stem DW	Root DW	Shoot:root ratio
0 mM	5·08	2·26	1·73	4·26
100 mM	3·39	1·57	0·75	6·64
S.E.	0·306	0·122	0·046	0·303
D.F.	4	4	4	4

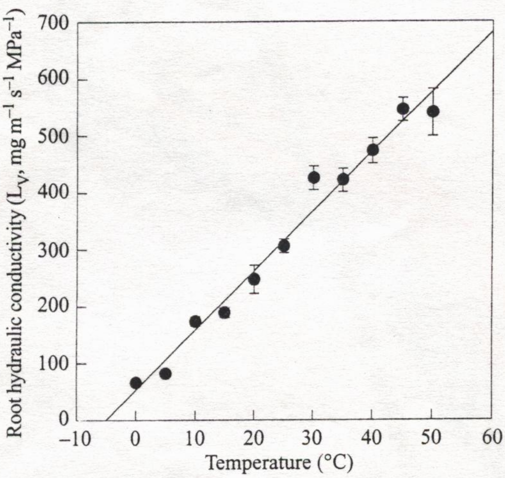

Fig. 4. Relationship between root temperature (T) *v.* root hydraulic conductivity (L_v) ($y = 10{\cdot}47x + 53{\cdot}56$, $r = 0{\cdot}99$) in tomato plants. Each point is the mean of eight measurements. Vertical bars represent S.E. of the mean.

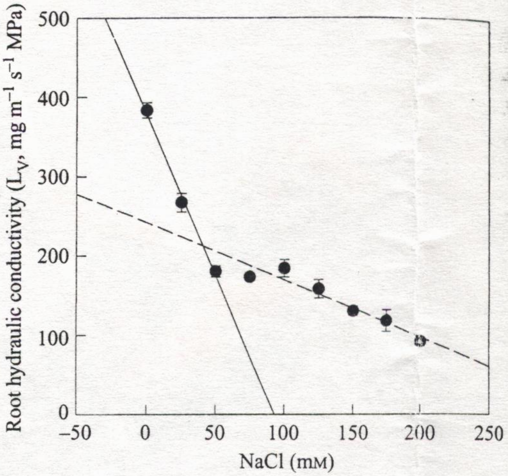

Fig. 5. Relationship between NaCl *v.* root hydraulic conductivity (L_v) in tomato plants. The continuous line illustrates the correlation when the salt concentrations applied were < 50 mM NaCl ($y = 378{\cdot}46 - 4{\cdot}060x$, $r = 0{\cdot}99$), the dotted line represents the correlation when the saline stress applied was > 50 mM NaCl ($y = 242{\cdot}10 - 0{\cdot}724x$, $r = 0{\cdot}96$). Each point is the mean of eight measurements. Vertical bars represent S.E. of the mean.

DISCUSSION

Leaf water potential, stomatal conductance and leaf relative water content values decreased in the salt-treated compared with control plants. This effect was very rapid, indicating that changes in the osmotic situation of the root medium quickly affect shoot water relations (Fig. 1).

Some evidence suggests that signals other than hydraulic signals alone communicate the soil water status to the shoot. Various researchers have discussed the possible involvement of plant hormones such as abscisic acid (Davies *et al.* 1986; Gollan *et al.* 1986). However, the strong correlation found in this paper between root hydraulic resistance and leaf water parameters (g_l and ψ_h) (Fig. 3) indicated that the reduction in ψ_h, g_l, RWC (Fig. 1) and also the inhibition of leaf growth (Table 1) were probably induced by the reduction of L_v caused by salt stress (Fig. 2).

Dry weights (leaves, stems and roots) were clearly lower in the saline treatment than in the control (Table 1). However, the shoot ratio increased in salt-treated plants (Table 1), indicating that there was a very substantial reduction in root growth under saline conditions, and that root quantity and distribution as well as hydraulic conductivity determine shoot development.

According to these data, it seems that the water flow through the root was the main factor controlling leaf water potential, stomatal conductance and also plant growth under saline stress. However, the study of salinity effects on the water flow through the roots must be made cautiously. For example, the root temperature effect on this water flow needs to be considered. In our results, there was a good correlation between root cooling and hydraulic conductivity for the whole range of temperatures (Fig. 4). In this instance, water absorption seems to be limited by the viscosity of the liquid around the roots. However, under saline conditions it is difficult to know if the reduction in the water flow through the root system is due only to changes in the water potential gradient across the root system or is the result of changes in hydraulic resistance by modifications of the root structure. Some researchers have shown that low levels of osmoticum affect water flux, but do not induce changes in the root's permeability (Shalhevet *et al.* 1976). Others, however, have found that long-term exposure to sodium chloride does affect the root structure (O'Leary 1969).

We have not found a significant correlation between the changes in water flow through the roots and the concentration of salts in the root medium (Fig. 5). In our opinion if this flow were only reduced by the water potential gradient, a linear correlation would be expected for the whole range of salt concentrations. However, it is possible to distinguish two different slopes in this correlation (Fig. 5). These two different phases indicate that there are some changes in the behaviour of the roots when the saline concentration is > 50 mM NaCl. This response was also observed in *Sorghum bicolor* under water stress (Cruz *et al.* 1992), and it was considered to be a tolerance mechanism of roots to severe water deficits. The question arises regarding what changes may have caused the root to increase its hydraulic resistance in response to salinity. This may have resulted from suberization of the endodermis (Nobel & Sanderson 1984) or by changes in membrane permeability (Lee-Stadelmann & Stadelmann 1976). The explanation of this radicular response to salt stress would be necessary to restrict the loss of water to the surrounding medium.

In conclusion, the results obtained in this work have shown that salt stress induced marked changes in root hydraulic resistance.These variations in root hydraulic conductivity, and the changes produced in root growth by saline stress, limited root water absorption and affected the water flow through the root system. In our opinion, these changes in water flow are sufficient to explain the signalling of the salt-stressed root to the shoot. The tolerance of tomato roots was increased by changes in the root structure when the saline stress was severe (salt concentrations > 50 mM NaCl).

The authors are grateful to M. D. Velasco, M. García, J. Soto and J. Soto-Montesinos for their assistance. The study was supported by the Scientific Cooperation Project between CSIC (España) and MINAGRI (Cuba).

REFERENCES

ALARCÓN, J. J., SÁNCHEZ-BLANCO, M. J., BOLARÍN, M. C. & TORRECILLAS, A. (1993). Water relations and osmotic adjustment in *Lycopersicon esculentum* and *L. pennellii* during short-term salt exposure and recovery. *Physiologia Plantarum* **89**, 441–447.

ALARCÓN, J. J., SÁNCHEZ-BLANCO, M. J., BOLARÍN, M. C. & TORRECILLAS, A. (1994). Growth and osmotic adjustment of two tomato cultivars during and after saline stress. *Plant and Soil* **166**, 75–82.

CRUZ, R. T., JORDAN, W. R. & DREW, M. C. (1992). Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum bicolor* L. following exposure to water deficit. *Plant Physiology* **99**, 203–212.

DAVIES, W. J. & ZHANG, J. (1991). Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology* **42**, 55–76.

DAVIES, W. J., METCALFE, J., LODGE, T. A. & DA COSTA, A. R. (1986). Plant growth substances and the regulation of growth under drought. *Australian Journal of Plant Physiology* **13**, 105–125.

GOLLAN, T., PASSIOURA, J. B. & MUNNS, R. (1986). Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology* **13**, 459–464.

LEE-STADELMANN, O. Y. & STADELMANN, E. T. (1976). Cell permeability and water stress. In *Water and Plant Life* (Eds O. L. Lange, L. Kappen & E. D. Schulze), pp. 268–280. New York: Springer-Verlag.

MARKHART, A. H. & SMIT, B. (1990). Measurement of root hydraulic conductance. *HortScience* **25**, 282–287.

NEUMANN, P. M., VAN VOLKENBURGH, E. & CLELAND, R. E. (1988). Salinity stress inhibits bean leaf expansion by reducing turgor, not wall extensibility. *Plant Physiology* **88**, 233–237.

NOBEL, P. S. & SANDERSON, J. (1984). Rectifier-like activities of roots of two desert succulents. *Journal of Experimental Botany* **35**, 727–737.

O'LEARY, J. W. (1969). The effect of salinity on permeability of roots to water. *Israel Journal of Botany* **18**, 1–9.

RAMAGE, R. T. (1980). Genetic methods to breed salt tolerance in plants. In *Genetic Engineering of Osmoregulation: Impact on Plant Productivity for Food, Chemicals and Energy* (Eds D. W. Rains, R. C. Valentine & A. Hollaender), pp. 311–318. New York: Plenum Press.

RAMOS, C. & KAUFMANN, M. R. (1979). Hydraulic resistance of rough lemon roots. *Physiologia Plantarum* **45**, 311–314.

SÁNCHEZ-BLANCO, M. J., BOLARÍN, M. C., ALARCÓN, J. J. & TORRECILLAS, A. (1991). Salinity effects on water relations in *Lycopersicon esculentum* and its wild salt-tolerant relative species *L. pennellii*. *Physiologia Plantarum* **83**, 269–274.

SCHOLANDER, P. F., HAMMEL, H. T., BRADSTREET, E. D. & HEMINGSEN, E. A. (1965). Sap pressure in vascular plants. *Science* **148**, 339–346.

SHALHEVET, J., MAAS, E. V., HOFFMAN, G. J. & OGATA, G. (1976). Salinity and the hydraulic conductance of roots. *Physiologia Plantarum* **38**, 224–232.

TENNANT, D. (1975). A test of a modified line intersect method of estimating root length. *Journal of Ecology* **63**, 995–1001.

TERMAAT, A., PASSIOURA, J. B. & MUNNS, R. (1985). Shoot turgor does not limit shoot growth of NaCl-affected wheat and barley. *Plant Physiology* **77**, 869–872.

VERDURE, M. (1981). Cultives sur laine de roche aux Pays-Bas. *PHM-Revue Horticole* **3**, 49–61.