Plant and Soil **166:** 75–82, 1994.

Growth and osmotic adjustment of two tomato cultivars during and after saline stress

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Received 1 December 1993. Accepted in revised form 30 June 1994

Key words: growth, osmotic adjustment, saline stress, solutes, *Lycopersicon esculentum*

Abstract

The effect of a short period of saline stress was studied in two phenotypically different cultivars, one of normal fruit-size (*L. esculentum* cv. New Yorker) and one of cherry fruit-size (*L. esculentum* var. *cerasiforme* cv. PE-62). In both cultivars the relative growth rate (RGR) and the leaf area ratio (LAR) decreased following salinisation. The leaf turgor potential (ψ_p) and the osmotic potential at full turgor (ψ_{os}) decreased to the same extent in both cultivars. However, the contributions of organic and inorganic solutes to the osmotic adjustment was different between cultivars. New Yorker achieved the osmotic adjustment by means of the Cl^- and Na^+ uptake from the substrate, and by synthesis of organic solutes. In the cherry cultivar organic solutes did not contribute to the osmotic adjustment, instead, their contribution decreased after salinisation. After the salt stress was removed, the water stress disappeared, the content of organic solutes decreased in plants of both cultivars and, therefore, their growth was not retarded by the diversion of resources for the synthesis of organic solutes. However, the toxic effects of the Cl^- and Na^+ did not disappear after removal of the salt stress, and the net assimilation rate (NAR) and the rate of growth (RGR) did not recover.

Introduction

The tomato, one of the more important and widespread crops in the world, is considered to be moderately salt tolerant (Maas, 1986). However, large differences are apparent in tolerance of different cultivars of *Lycopersicon esculentum* which can be used for comparative physiological studies that should permit faster progress in breeding programmes (Hassan and Desouki, 1982). Within this species the commercial production of cherry tomatoes is increasing (Hobson and Bedford, 1989) and some workers have pointed out that these small-fruited tomato varieties are more salinity-tolerant than are the normal-fruited ones (Anastasio et al., 1987; Shannon et al., 1987). According to the salinity-threshold (maximum electrical conductivity (EC) value without yield reduction) and slope (yield decrease per unit EC increase) parameters, determined from the yield-EC response curves, Caro et al. (1991) observed that cherry tomato cultivars were the more salt-tolerant.

Genetic variability within a species offers a valuable tool for studying mechanisms of salt tolerance. One of these mechanisms depends on the capacity for osmotic adjustment. A general feature of many plants growing in a saline environment is that they maintain turgor by accumulation of inorganic solutes in their cells (Flowers et al., 1977; Yeo, 1983). However, this accumulation of ions can produce problems of mineral toxicity and nutritional imbalance (Blum, 1986). Which of these factors (water stress or ion excess or imbalance) results in a limitation of growth can depend on the species, the cultivars or the degree of saline stress. One approach, proposed by Munns et al. (1982), to distinguish between the effect on growth produced by water deficit and by ion excess is to study changes in growth after a decrease in external NaCl because the water stress would disappear while the tissues would be still high in ions. In accordance with this approach, we studied the effects during a short period of saline stress.

Although the relationship between salt tolerance and osmotic adjustment is not clear, various workers have shown that the way in which the osmotic adjustment is achieved will determine, at least partially, the salt tolerance of a species or genotype (Richardson and McCree, 1985). Osmotic adjustment is determined by two factors: the capacity to adjust the water relations and the capacity for accumulation of osmotic solutes. Cuartero et al. (1992) reported the water content and succulence of six accessions of wild and cultivated tomato during saline stress, they concluded that succulence is important to salt-tolerance in tomato; however they did not find salinity increased the ratio of fresh to dry weight in *L. esculentum*. Alarcón (1992) studied the effects of salinity on water relations through the growing season in two tomato cultivars (cherry and normal-fruited). Despite great morphological differences between these tomato cultivars, the effects of salt on leaf water relations were similar throughout the growing season. We consider, according to these results, that both cultivars have a similar capacity to adjust their water relations through alterations of the cellular water content; therefore, the differences in salt tolerance among these cultivars would require a different capacity for accumulation of osmotic solutes in leaf tissues. Marschner (1986) indicated that the osmotic adjustment based on the synthesis of organic solutes requires an important energy expenditure, while Flowers et al. (1977) argued that the accumulation of ions in the vacuole provide energetically "cheap" solutes for osmotic adjustment. Since the different contribution of inorganic and organic solutes to osmotic adjustment has important implications for energy balance (Wyn Jones, 1981), it is necessary to take into account not only the degree of osmotic adjustment but also the type of solutes contributing to the osmotic adjustment in order to achieve a deeper understanding of the physiological differences among tomato cultivars with different salt tolerance.

Materials and methods

Plant material and treatments

The experiment was conducted on tomato plants of two very different cultivars, one of normal fruit-size (*L. esculentum* cv. New Yorker) and another of small (Cherry) fruit-size (*L. esculentum* var. *cerasiforme* cv PE-62). Tomato seeds were germinated and grown in trays of washed silica sand in a growth chamber. Environmental conditions during the germination period were dark, 28°C and 90% RH. During plant development there was 16 h illumination with the maximum/minimum photosynthetically active radiation (PAR) 245/81 μmol m^{-2} s^{-1}. Illumination/dark average temperatures and relative humidity were 30/17 °C and 60/75 % respectively.

Plants were watered daily with full strength Hoagland solution from two weeks after sowing. When the plants developed 5–6 true leaves (30 days after germination) salt treatments were applied using nutrient solution with 0, 70 or 140 m*M* NaCl. The NaCl levels in 70 and 140 m*M* treatments were reached by daily increments of 35 m*M* NaCl. The electrical conductivities of the nutrient solutions were 1.45, 7.23 and 12.61 dS m^{-1}, respectively.

After 17 days of saline stress, the sodium chloride was removed from the roots by rinsing with distilled water. Nutrient solutions were renewed daily. Recovery time using NaCl-free nutrient solutions lasted an additional 8 days.

The design of the experiment was completely randomized with 3 replications of 54 plants per replicate (2 cultivars × 3 salt treatment × 3 harvest period × 3 plants per harvest).

Growth parameters

Before the start of treatments, at the end of the saline period and at the end of the recovery period, three plants per replicate (27 plants per cultivar) were harvested, and measurements of root, stem and leaf fresh and dry weights were taken. Leaf area was also measured using a Delta-T leaf area meter.

To compare the effects of saline stress on plant growth, relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) for each period of the experiment under different levels of salinization were calculated. Leaf area ratio (LAR) was calculated as the leaf area per unit whole plant dry mass. Data from consecutive samplings were used to compute NAR by the equation $(W_2 - W_1)\ (t_2 - t_1)^{-1}\ (L_2 - L_1)^{-1}$ and RGR by the equation $(\ln W_2 - \ln W_1)\ (t_2 - t_1)^{-1}$ where, W = mean total plant dry mass (mg for NAR; g for RGR), t = time (days), L = mean leaf area (cm^2).

Plant water relations

Each three days during the salinization period and each two days during the recovery period, the leaf turgor potential (ψ_p) was estimated as the difference between

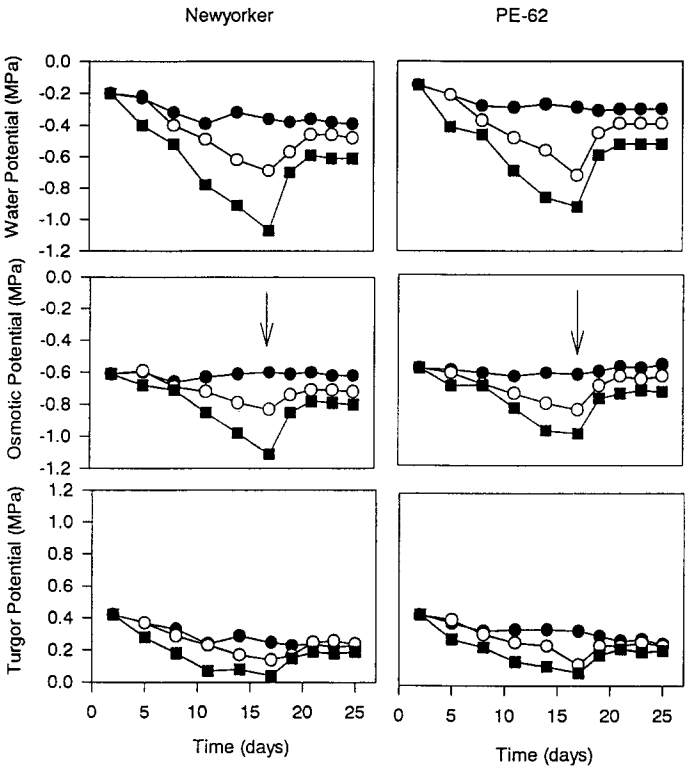

Fig. 1. Course of leaf water potential (ψ_h, MPa), leaf osmotic potential (ψ_s, MPa) and leaf turgor potential (ψ_p, MPa) at minimum irradiance for *L. esculentum* (cv New Yorker) and *L. esculentum* var. *cerasiforme* (cv PE-62) in control (●) and saline (○,70; ■,140 m*M* NaCl) treatments during the experimental period. Arrows indicate the beginning of the recovery period. Each point is the mean of 6 measurements. The maximum SE (Standard Error) of the mean value was 0.02, they were not printed because they are smaller that the symbols.

the leaf water potential (ψ_h) and the leaf osmotic potential (ψ_s) measured at minimum PAR level on six plants of each genotype and treatment. Leaf water potential was estimated using a pressure chamber (Soil Moisture Equipment Co., Santa Barbara, CA, USA) according to Scholander et al. (1965). Leaf osmotic potential was measured using a psychrometer Wescor HR-33T according to Neumann and Thurtell (1972).

Leaf osmotic potential at full turgor (ψ_{os}) was estimated by pressure-volume analysis at each harvest. The leaves excised were in the dark, placed in plastic bags with their petioles dipping in distilled water, and allowed to reach full turgor overnight. Pressure-volume curves were obtained by periodic measurement of leaf weight and balance pressure as leaves dried on the bench.

Osmotic contribution of solutes

Leaves were washed in distilled water, oven dried at 70 °C, ground and stored for inorganic solute analyses. For organic solutes, fresh material was lyophilized and stored at -20 °C.

Foliar Na^+ and K^+ were determined in dilute nitric-perchloric acid (2:1) extracts using atomic absorption spectroscopy. Cl^- and NO_3^- were analyzed in aqueous extracts by potentiometric titration with $AgNO_3$ and by Lambert and Du Bois (1971) methods, respectively.

Extraction of soluble sugars and organic acids was as described by Bourgeais-Chaillou and Guerrier (1992). Extracts were analyzed for soluble sugars using the method of Morris and Arthur (1948) and for organic acids by a HPLC system using the procedure of Timpa et al. (1986). Free aminoacids were extracted with phosphate buffer 50 m*M* in presence of PVP 1% and Triton X-100 0.01% and determined in autoanalyzer using the ninhydrin postcolumn reaction.

The contribution of solutes to total ψ_{os} was calculated according to Munns and Weir (1981), from the relative dry weight (RDW, kg m^{-3}) at saturation [dry weight / (saturated weight - dry weight)] for each sample, the solute concentration on a dry-weight basis (C, g kg^{-1}), the molecular weight of each solute (M, g

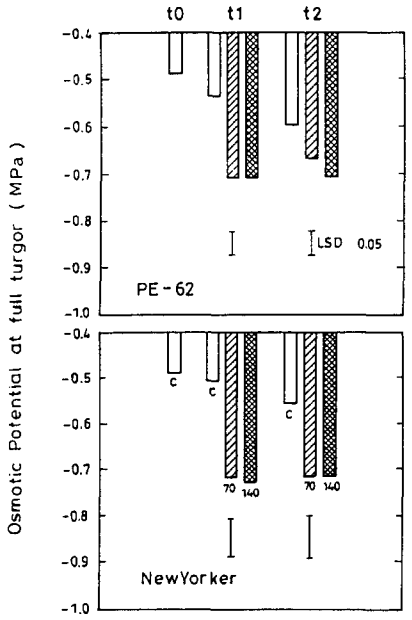

Fig. 2. NaCl effect on the osmotic potential at full turgor (ψ_{os}, MPa) in leaves of *L. esculentum* (cv New Yorker) and *L. esculentum* var. *cerasiforme* (cv PE62) at three different times: t0, before beginning treatments; t1, at the end of salinization period in plants treated with 0 (C), 70 and 140 m*M* NaCl; and t2, at the end of recovery time in plants proceeding of the three salt treatments. $LSD_{0.05}$ calculated by Student-Newman-Keuls Test.

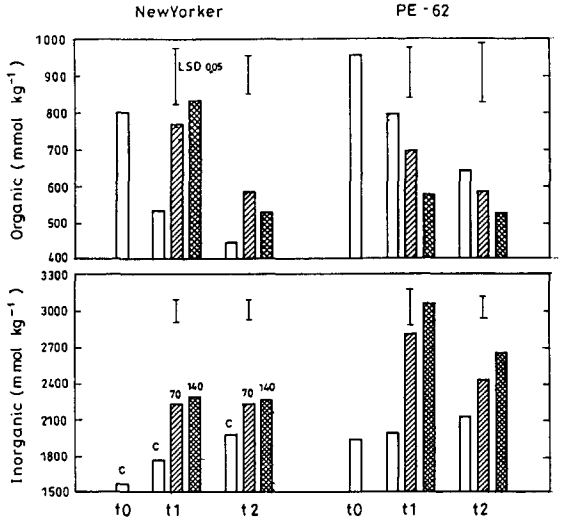

Fig. 3. NaCl effect on total inorganic and organic solute contents (mmol kg^{-1}DW) in leaves of *L. esculentum* (cv New Yorker) and *L. esculentum* var. *cerasiforme* (cv PE-62) at three different times: t0, beginning treatments; t1, at the end of salinization period in plants treated with 0 (C), 70 and 140 m*M* NaCl, and t2, at the end of recovery time in plants proceeding of the three salt treatments. $LSD_{0.05}$ calculated by Student-Newman-Keuls Test.

mol^{-1}), and the van't Hoff relation (using a RT value for 25 °C of 0.002479 m^3 MPa mol^{-1}, Nobel, 1983). It was assumed that solutes behaved as ideal osmotica.

$$\psi_{os}\text{calculated} = -0.002479 \times \text{RDW} \times \text{C} \times 1/\text{M} \quad (1)$$

Results

During the salinization period, the leaf turgor potential (ψ_p) decreased significantly in 70 and 140 m*M* NaCl (Fig. 1). There was a direct relationship between the degree of the saline stress applied and the decrease of water stress (decrease of leaf turgor pressure) measured in the plants, therefore, the plants of the treatment 140 m*M* suffered a greater water stress than the plants of the treatment 70 m*M*. After the salt stress was removed, there were not significant differences in the values of ψ_p between the control and the pretreated plants. The water stress disappeared. The leaf water potential (ψ_h) and the leaf osmotic potential (ψ_s) values decreased during the salinization period and were partially recovered when the salts were removed from the medium (Fig. 1).

In the control plants of both genotypes, the relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) varied with plant age: RGR and LAR decreased, while the values of NAR increased (Table 1). The values of RGR decreased in both cultivars under saline stress. However the effect on LAR and NAR values was different during the salinization period compared to the recovery period. With salt stress there was a significant reduction of LAR, but NAR values were maintained. During recovery NAR decreased while the values of LAR were not affected in the treated plants (Table 1).

The ψ_s values were lower in the salt-stressed than control plants in both genotypes (Fig. 2). In cv. New Yorker similar values were obtained after both salt stress and recovery, while in cv PE-62 the ψ_{os} increased slightly during the recovery time. The behaviour of ψ_{os} reflected the total content of the measured solutes. A linear relationship was obtained between leaf osmotic potentials at full turgor (measured from pressure-volume curves) and osmotic potential calculated from the total contribution of the individual solutes. This was found across both genotypes and all treatments, the slope being near to unity. The regression equation was $y = 0.81x - 0.14$ ($r^2 = 0.830$, $p = 0.089$).

Table 1. NaCl effects on relative growth rate (RGR, g g^{-1} day^{-1}), net assimilation rate (NAR, mg cm^{-2} day^{-1}) and leaf area ratio (LAR, cm^2 g^{-1}) in tomato plants of *L. esculentum*, cv New Yorker (NY), and *L. esculentum* var cerasiforme, cv PE-62 (PE), exposed for 17 days to different NaCl levels (t0-t1) and recovered for 8 days (t1-t2). Means within a column for each time that do not have a common letter are significantly different by $LSD_{0.05}$ test

		RGR		NAR		LAR	
Time	m*M* NaCl	NY	PE	NY	PE	NY	PE
t0 - t1	0	0.12a	0.13a	0.38a	0.38a	190a	173a
	70	0.11b	0.11b	0.40a	0.41a	157b	149b
	140	0.10c	0.09c	0.43a	0.42a	136c	134c
t1 - t2	0	0.08a	0.08a	1.12a	1.99a	149a	124a
	70	0.06b	0.07b	0.96b	1.85b	153a	131a
	140	0.06b	0.06b	0.91b	1.71c	140a	130a

Table 2. Contribution of inorganic (Na^+, K^+, Cl^-, NO_3^-) and organic (sugars, SS, organic acids, OA, aminoacids, AA, proline) solutes (MPa $\times$ 10^{-1}) to leaf osmotic potential at full turgor, in two tomato cultivars (New Yorker, NY, and PE-62, PE) at three different times: t0, before beginning treatments, t1, at the end of salinization period and t2, at the end of recovery period. Means within a file for each time and cultivar that do not have a common letter are significantly different by $LSD_{0.05}$ test

Time	t0	t1			t2		
NaCl treatment (m*M*)	0	0	70	140	0	70[z]	140[z]
NY							
Na	-0.07	-0.04b	-1.32a	-1.34a	-0.09b	-1.03a	- 0.95a
K^+	-1.61	-2.05a	-2.09a	-1.94a	-2.20a	-2.19a	-1.87b
Cl_-	-0.10	-0.09b	-1.34a	-1.20a	-0.14c	-1.13b	-1.26a
NO_3^-	-1.22	-1.56a	-0.93b	-1.09b	-1.72a	-1.02b	-1.17b
SS	-0.34	-0.25c	-0.54b	-0.80a	-0.14a	-0.25a	-0.21a
OA	-0.86	-0.51b	-0.95a	-0.74ab	-0.63a	-0.87a	-0.68a
AA[x]	-0.32	-0.38a	-0.34a	-0.30a	-0.16a	-0.28a	-0.33a
Proline	-0.01	-0.01c	-0.12b	-0.19a	-0.0la	-0.01a	-0.01a
PE							
Na^+	-0.01	-0.0lc	-0.94b	-1.18a	-0.06c	-0.91b	-1.16a
K^+	-1.87	-1.96a	-1.93a	-1.98a	-1.96a	-1.89a	-1.74a
Cl^-	-0.10	-0.11c	-1.99b	-2.26a	-0.11c	-1.36b	-1.64a
NO_3^-	-1.62	-1.96a	-1.08b	-1.01b	-1.76a	-0.96b	-1.07b
SS	-0.24	-0.30a	-0.28a	-0.23a	-0.15a	-0.17a	-0.21a
OA	-1.20	-1.02a	-0.72b	-0.65b	-0.76a	-0.69a	-0.57a
AA[x]	-0.36	-0.30b	-0.39a	-0.23b	-0.28a	-0.35a	-0.34a
Proline	-0.01	-0.01b	-0.09a	-0.10a	-0.01a	-0.02a	-0.01a

[z] Salt levels applied during t1.

[x] Total free aminoacids except proline.

The concentrations of organic and inorganic solutes varied with the age of the plant, the cultivar, and the treatment. In the control plants, the concentration of total leaf organic solute showed a tendency to decrease as the plants aged. The opposite pattern was noted for total leaf inorganic concentration (Fig. 3). Under saline stress, both cultivars showed an increase in total leaf solute concentration. In the cherry cultivar, this increment was due solely to increases in inorganic solutes, the organic solute content decreased with salinity (Fig. 3). However, in New Yorker, salinity induced an increment in both inorganic and organic solute concentrations (Fig. 3). At the end of the recovery period an increment in the leaf total solute concentrations was also observed in the salt stressed plants. In this period, the ψ_{os} values decreased in both cultivars only by an increment of inorganic solutes while the organic solute concentration was not affected by the saline treatments (Fig. 3).

The contributions of different inorganic ions to ψ_{os} varied with salinity (Table 2). K^+ was the only solute that did not change significantly its contribution toψ_{os} under salinization in either cultivar: NO_3^- contribution decreased significantly, specially in PE-62 (Table 2). The increase of the inorganic solute contribution to ψ_{os} was only due to the accumulation of Na^+ and Cl^-. The leaf Cl^- contribution in the salt treated plants of PE-62 was much higher than that in New York. In PE-62 the Na^+ and Cl^- contributions were higher in 140 m*M* than in 70 m*M* NaCl, while in New Yorker Na^+ and Cl^- were similar in both treatments (Table 2).

The increment of the organic solute contribution to ψ_{os} with salinity in New Yorker was mainly due to sugars and organic acids while in PE-62 was due to organic acids (Table 2). Only proline increased in both cultivars, although its contribution to ψ_{os} was very low. After the recuperation period, the leaf organic solute contributions had not changed significantly compared with the control plants of both cultivars (Table 2).

Discussion

There is evidence from recent years that leaf expansion is reduced a low water potentials in the growth medium because of signals arrising in the roots, and that a simple inference that reduced leaf turgor implies that the plants are water stressed is not valid. Munns (1993) argued that the steady state growth rate is independent of leaf turgor and it is altered only by treatments that alter the soil water status. Termaat et al. (1985) found that shoot growth was reduced when barley and wheat root systems were inmersed in salt solution even though turgor was maintained by applying pressure to the solution containing the roots. However, Kramer (1988) argued that it is not surprising that cell enlargement is not always closely correlated with turgor because it depends on metabolic processes, as well as on the physical processes affecting the water supply and cell turgor. Neumann et al. (1988) showed that in one species at least turgor remain an important factor in the control of leaf growth. The mechanism by which salt reduces leaf area expansion needs to be resolved, but we consider at this moment that measurements of leaf water relations and osmotic adjustment have value in predicting or explaining the growth rate of salt-affected plants and that reduced leaf turgor implies that the plants are water stressed.

Plant growth analysis has been applied to analyze the effects of salinity on plants. Some reports showed that salinity affected LAR, but not NAR (Curtis and Läuchli, 1986), indicating that the growth limiting factor was leaf expansion. In contrast, others reported that the decrease of RGR was correlated with NAR, but not LAR (Cramer et al., 1990), indicating that photosynthesis may be limiting growth. In our experiment, the fact that RGR decreased significantly shows that growth of the plants was reduced by salinity. The growth was limited by water stress and/or ion excess in both cultivars. The water stress, produced during the period of salinization, would have limited the growth of the expanding tissues. This effect was reversible during the recovery period, when the water stress disappeared (recovery of leaf turgor pressure, Fig. 1). For this reason, LAR decreased significantly during the salinization period (Table 1). However, the effect produced by accumulation of ions on the metabolism in the mature tissues was not reversible, therefore, NAR was affected during the recovery period although there was no water stress during this period (Table 1). The cellular expansion rate is affected more rapidly than the photosynthesis rate in salty conditions.

Wilson et al. (1989) indicated that osmotic adjustment is accounted for by decreases in the saturated mass/dry mass ratio, increases in the apoplastic water content, and direct solute accumulation. No significant changes in the two first parameters (data not shown) were observed; therefore, in our experimental conditions the ψ_{os} reductions observed in plants of both cultivars under saline stress were the result of the accumulation of solutes. The capacity for accumulation of osmotic solutes in leaf tissue seems limited (Tyree

and Jarvis, 1982). This limited capacity is shown by both cultivars, since total solutes there was little or no increase in with increasing salinity from 70 to 140 m*M*, as reflected also by a plateau in the ψ_{os} measured (Fig. 2). This limited osmotic adjustment was not sufficient to avoid water stress in the treated plants, but was sufficient to prevent complete loss of turgor pressure (Fig. 1). The osmotic adjustment was still shown by the plants during the recovery period (Fig. 2); for this reason the leaf water and the leaf osmotic potential values did not totally recover in the pre-treated plants (Fig. 1).

The slope of the relationship between the ψ_{os} measured by the pressure-volume curves and the ψ_{os} calculated by the total contribution of analyzed individual solutes was near unity, this indicates that the solutes which have been considered are the major components of the osmotic adjustment in tomato plants grown at both control and salt treated conditions.

The declines in ψ_{os} in both salt treated and recovering plants were mainly due to the Na^+ and Cl^- ions (Table 2), as found by Gibbs et al. (1989), who reported that in salt treated plants, the elements provided in the saline water were generally the major components for osmotic adjustment. PE-62 showed a higher Cl^- accumulation capacity in leaves than New Yorker, this higher accumulation could have induced greater decline in the NO_3^- found in PE-62. The fact the K^+ contribution to the ψ_{os} did not decrease under saline conditions indicates that both tomato cultivars are able to maintain a high K^+ selectivity, probably through efficient K^+/Na^+ selectivity at the root endodermis.

The largest differences found between the cultivars was in the contribution of organic solutes to osmotic adjustment (Table 2). Thus New Yorker achieved the osmotic adjustment by means of the Cl^- and Na^+ uptake and by the synthesis of organic solutes. The proportional increment of sugar with the different levels of salinity showed by this cultivar indicates that the low molecular weight carbohydrates are the main organic solutes involved in osmotic adjustment, as reported by Greenway and Munns (1980) in glycophytes subjected to saline stress. The other organic solute that increased proportionally with the salt level was proline, although its contribution to the osmotic adjustment was very low. However, it has been suggested that proline is concentrated in the cytoplasm and it might be an important "compatible" solute (Prat and Fathi-Ettai, 1990). Contrary to the response of New Yorker, in the cherry cultivar, PE-62, the organic solutes did not contribute to the osmotic adjustment, rather, they decreased their contribution at higher salinity (Table 2). This decrease in the salt treated plants suggests an impaired respiration and a decreasing energy supply (Bellinger and Larher, 1987). It also can be related with the uptake and foliar accumulation of Cl^- (Hamza, 1980).

When the salt stress was removed, the plants did not accumulate organic solutes (Table 2) and, therefore, their growth should not be limited by the energy costs involved in organic solute synthesis. However, the toxic effects of the Cl^- and Na^+ and nutritional alterations did not disappear during this time. We conclude that the most of the effects induced by salt stress (water stress and accumulation of organic solutes) are eliminated when the salts are removed; only the effects produced by accumulation of ions on the metabolism in the mature tissues are not reversible.

Because osmotic adjustment by salt accumulation is less energy and carbon demanding than adjustment by organic solutes (Wyn Jones, 1981), the effect of salinity on plant growth should be lower in the cherry cultivar than in New Yorker. This could explain the higher degree of salt tolerance shown by PE-62 when the NaCl treatments were applied long-term (Gough and Hobson, 1990). However, it is important to take into account that several factors affect the salinity tolerance of a cultivar, such as the salinity level, the exposure time to salt stress and the plant age (Cruz and Cuartero, 1991; Hoffman and Jobes, 1978). These factors could explain the similar growth reductions of both cultivars observed in our experimental conditions (salt stress applied short-term on young plants). It is possible that the young cherry tomato (PE-62) was unable to sequester ions efficiently in the vacuole. Therefore, they accumulate the salts within the cytoplasm, leading to toxicity and inhibition of growth. By contrast, in New Yorker ions are excluded effectively, but the growth is decreased because of diversion of resources into accumulation of organic solutes.

Acknowledgements

The authors are grateful to Mrs M D Velasco, Mrs M Rojo and Mrs A Santacruz for their assistance. The study was supported by CICYT (Comision Interministerial de Ciencia y Tecnología), included in project AGF92–0260.

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Section editor: T J Flowers