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Effects of Salinity on Growth and Accumulation of Organic and Inorganic Ions in Cultivated and Wild Tomato Species

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Additional index words. *Lycopersicon esculentum, L. cheesmanii, L. peruvianum, L. pennellii,* salt tolerance, selection

Abstract. **The salt tolerances of a cultivated tomato (*Lycopersicon esculentum* L. cv. Heinz 1350) and three wild species [*L. cheesmanii* (Hook) C.H. Mull, *L. peruvianum* (L.), and *L. pennellii* (Cornell) D'Arcy] were determined in both sand and solution cultures. Curvilinear and two-piece linear methods were used to obtain response curves for fresh and dry weights of shoots. In solution cultures containing 0, 50, 100, and 150 mM added salt composed of 1:1 molar ratio of NaCl and $CaCl_2$, 'Heinz 1350' was as salt-tolerant as any of the wild species. On the basis of relative decreases in vegetative dry weight, ecotype 1400 of *L. cheesmanii* was more sensitive to salt than ecotype 1401. After 4 weeks growth in sand cultures irrigated with nutrient solutions containing 0, 12.5, 25, 50, 75, and 100 mM added salts (5:1 molar ratios of NaCl and $CaCl_2$), *L. pennellii* had higher relative salt tolerance than the other species. After 14 weeks, the cultivated species and *L. pennellii* were more sensitive at low salinity than the other two species. However, relative yield decreases with increasing salinity were not significantly different between the cultivated tomato and the 1401 ecotype of *L. cheesmanii* at higher salt concentrations. *L. peruvianum* and *L. pennellii* accumulated less leaf Cl^- and more leaf Na^+ than the other species. Significant differences in the partitioning of ions between mature and developing leaves were found for all species. The physiological mechanisms involved in tolerance at moderate salinities may differ from those required for survival at high salinity.**

The improvement of salt tolerance in agricultural species has been promoted as an agronomic approach to the exploitation of large areas of saline soils and the efficient use of the relatively abundant saline water supplies that currently have little agricultural value (6, 14). Genetic variability for salt tolerance is quite sufficient for breeding purposes in some species (5); in others, it is limited and there is a need to increase variability through interspecific crosses. Lyon (11) suggested that salt tolerance in the cultivated tomato might be improved by transferring genes from related wild species. High salt tolerance has been reported in several wild relatives of the cultivated tomato (4, 11, 16, 18, 23).

The purpose of our study was to determine the differences in salt tolerance among four tomato species under similar conditions and to detect physiological differences that might provide

Received for publication 11 Apr. 1986. This research was supported by a grant from the United States–Israel Binational Agricultural Research and Development Fund (BARD). We thank Charles Rick of the Univ. of California, Davis, for providing seeds of the wild species that were used in this study and Donald Layfield and Catherine Grieve of the Salinity Laboratory for their analytical help. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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insight into the mechanisms responsible for the differences in tolerance.

Materials and Methods

Species used in these studies included *Lycopersicon esculentum* cv. Heinz 1350 (Le), two ecotypes of *L. cheesmanii*, accessions 1400 (Lc-1400), and 1401 (Lc-1401), *L. peruvianum* and *L. pennellii* accession Atico (La), previously classified as *Solanum pennellii* Cor. Seeds of of the wild species were soaked in 2.7% NaOCl for 45 min and rinsed thoroughly in distilled water for 30 min before germination. Le seed was pretreated with 2.7% NaOCl for only 15 min prior to germination. Seeds were germinated in the dark on filter paper soaked with 0.1 mM $CaCl_2$ and after emergence the seedlings were transformed to aerated nutrient solutions. Germination and early seedling growth rates (up to two to three leaves) among the wild species are much slower than those of the cultivated species, making it difficult to establish seedling populations of uniform size and maturity. Plants of the cultivated species were about 3 weeks younger than the wild species at the time of transplanting, but were still slightly larger in size and had the same number of leaf axes.

Salt tolerance in solution cultures. In Oct. 1981, seedlings of the cultivated species (4-week-old) and the wild species (6-week-old) were transferred to 60-liter solution culture containers in the greenhouse. There were 20 containers, each with four plants (replications) of one of five entries (Le, Lc-1400, Lc-1401, Lp, and La). Nutrient solutions contained 6 mM KNO_3, 6 mM $Ca(NO_3)_2$, 3 mM $MgSO_4$, 0.18 mM KH_2PO_4, 0.1 mM Fe as diethylene-triamine pentaacetate, 46 μM H_3BO_3, 9 mM $MnCl_2$, 0.8 μM $ZnSO_4$, 0.3 μM $CuSO_4$, and 0.1 μM H_2MoO_2. After 1 week, salinity treatments were initiated by adding 12.5 $mmol \cdot liter^{-1} \cdot day^{-1}$ each of NaCl and $CaCl_2$ to the culture solutions. Salinity treatments of 0, 50, 100, and 150 mM total NaCl + $CaCl_2$ were established. Electrical conductivities of the treatment solutions (κ_i) averaged 1.0, 7.9, 14.2, and 20.7 $dS \cdot m^{-1}$, respectively. Nutrient solution pH was maintained between 6.0 and 6.5 with additions of H_2SO_4. Average daily maximum and minimum temperatures in the greenhouse during the study were 31° ± 3°C and 18° ± 1°, respectively.

Fresh and dry shoot and root weights were measured 4 weeks after the last salination. Plants were flowering at the time of harvest. Roots were given three successive 20-sec rinses in fresh solutions of 0.5 mM $CaSO_4$, and were centrifuged at $300 \times g$ for 10 min in wire baskets before weighing.

Salt tolerance in sand cultures. Salt tolerance tests were conducted in 18 outdoor sand-culture plots each measuring 1.5 × 3 m and filled to a depth of 2 m with medium-textured river sand. Each plot was irrigated through a recycling flood system from separate 4000-liter reservoirs. Three 4- to 6-week-old plants each of Le, Lc-1401, Lp, and La were transplanted into each plot in July 1982. Salt treatments were established by adding NaCl and $CaCl_2$ (5:1 molar ratio) at a rate of 25 $mmol \cdot liter^{-1} \cdot day^{-1}$ to final concentrations of 0, 50, and 100 mM, and average κ_i of 1.9, 8.6, and 13.4 $dS \cdot m^{-1}$, respectively. Nutrient solutions were recycled either once or twice daily to provide two irrigation frequency treatments. Thus, the experiment had a split-split plot design with 4 species × 3 salinities × 2 irrigation frequencies, with three replications. About 400 liters of solution were applied to the surface of each plot during each irrigation. Salinity and pH were measured and adjusted every other day, and water loss due to plant uptake and evaporation was replenished daily. Average daily maximum and minimum day temperatures were 34° ± 4°C and 17° ± 3°, respectively, during the experiment. Plants were harvested 12 weeks after salination. Fruit and shoot fresh weight and shoot dry weights were measured.

Slight modifications were made in the sand culture tests in the following year. Six 4- to 6-week-old plants of Le, Lc-1401, Lp, and La were transplanted into the 18 plots in May 1982. Salt treatments were established with three replications by adding NaCl and $CaCl_2$ (5:1 molar ratio) at a rate of 25 $mmol \cdot liter \cdot day^{-1}$ to final concentrations of 0, 12.5, 25, 50, 75, and 100 mM. The average κ_i of these solutions were 2.0, 3.6, 5.5, 8.6, 11.8, and 13.5 $dS \cdot m^{-1}$, respectively. Plants were irrigated twice daily. After 4 weeks salination, three plants of each species were harvested. Fresh and dry shoot weights were measured and leaf samples were taken. Final harvest was conducted in August after about 14 weeks of salination. Fruit harvest was conducted as necessary in the final 2 weeks before the experiment was ended. Fresh and dry shoot weights and fresh fruit weight were measured. Average daily maximum and minimum temperatures during the experiment were 34° ± 5°C and 16° ± 3°, respectively.

Leaf and root analyses. In solution culture studies, composite leaf samples were taken of developing and mature leaves. Developing leaves were defined as those leaves not fully expanded and located within two to three nodes of the branch apex. Mature leaves were chosen as fully expanded, nonsenescent leaves. Only mature-leaf samples were taken in the sand culture studies. Leaf tissues from each experiment were analyzed for Na^+, Ca^{2+}, K^+, Mg^{2+} and Cl^-. Cations were measured by atomic absorption spectrophotometry on nitric–perchloric acid digests and Cl^- was determined by potentiometric titration of nitric–acetic acid extracts (3). Free proline was extracted in sulfasalicyclic acid and determined colorimetrically with acid-ninhydrin (2). Quaternary ammonium compounds were estimated colorimetrically on periodate-developed acid extracts in the solution culture study (9).

Results

Salt tolerance in solution culture. Salinity decreased total fresh and dry weights of shoots and roots in all tomato species (Table 1). Under nonsaline conditions, both ecotypes of Lc had significantly higher fresh and dry shoot weights than La, but were not statistically different from Lp or the cultivated Le. Salt concentrations of 50 mM did not affect the shoot or root growth of the cultivated species adversely and average dry weight was about 6% higher than controls. Slight stimulation of vegetative growth of cultivated tomatoes in solution cultures at salt concentrations up to 100 $mg \cdot liter^{-1}$ Cl have been reported elsewhere (15).

Salinity stimulated an increase in the root : shoot ratio in all species except La. Dry weight percentage in shoots were highest in Lp and lowest in Le and increased with salinity in both of these species.

Salt tolerance curves estimated by piecewise-linear methods (12) were not significantly different from those calculated by a nonlinear least-squares inversion method (25). Values were determined for Y_{max} (maximum theoretical yield), threshold (maximum salinity without yield reduction), absolute and relative slopes (yield decline per unit salinity increase), C_0 (salinity that reaches zero), and C_{50} (salinity at which calculated yield is 50% of the maximum) (Table 2). Regardless of the methods used to measure salt tolerance, Le was as tolerant as any of the wild species as determined by vegetative growth in solution culture. Le has the highest threshold, C_0 and C_{50} values. Lc-1400 was

Table 1. Shoot and root growth of four species of tomato grown in solution cultures of different salinity

Species	Salinity[z]	Shoot	Root	Total	Root : Shoot	Dry wt[y]
Lycopersicon esculentum (Le)	0	42.0	24.9	66.9	0.59	6.7
	50	44.3	26.4	70.6	0.59	6.5
	100	21.9	19.1	41.0	0.88	7.3
	150	18.9	21.8	40.7	1.16	8.5
L. cheesmanii (Lc-1401)	0	56.5	24.5	81.1	0.43	8.9
	50	50.9	28.3	79.2	0.56	7.6
	100	17.5	19.7	37.2	1.12	7.6
	150	9.8	10.1	19.9	1.15	9.2
L. cheesmanii (Lc-1400)	0	51.3	33.2	84.5	0.65	8.7
	50	16.5	13.7	30.2	0.83	6.0
	100	10.8	15.9	26.7	1.46	6.7
	150	4.2	6.9	11.1	1.63	7.9
L. peruvianum (Lp)	0	45.1	27.2	72.3	0.60	10.2
	50	26.9	15.7	42.6	0.59	10.4
	100	14.5	13.9	28.3	0.96	10.5
	150	15.5	15.5	30.9	1.00	10.9
L. pennellii (La)	0	31.5	14.2	45.9	0.46	9.7
	50	26.6	10.3	36.8	0.39	9.0
	100	12.0	9.2	21.1	0.77	9.3
	150	8.2	7.3	15.5	0.53	8.9

[z]Concentration of NaCl and $CaCl_2$ salts added to the nutrient solutions on a 1:1 molar basis.
[y]Percentage of dry weights of shoots.

the most sensitive entry and, as has been reported elsewhere, was not as tolerant as Lc-1401 (18, 19).

Salt tolerance in sand cultures. Salinity reduced both vegetative and fruit yields in sand culture and showed significant interaction ($P = 0.01$) with irrigation frequency. Because dry weights could not be determined conveniently, vegetative growth is given in Table 3 as fresh weight so that comparisons can be made with fruit yield. Total plant fresh weights, which included fruit weight, were higher for Le and Lc-1401 than for Lp and La regardless of salinity treatment.

Two daily nonsaline irrigations increased total plant weight of Lc-1401 and Le compared to one daily irrigation (Table 3). This suggests that a single daily irrigation was inadequate to support the optimum water requirements of these large, rapidly growing species. The slower-growing species, Lp and La, had no increase in growth as a result of an additional daily irrigation.

Fruit yield in Le averaged about 62% of the total fresh weight, regardless of salinity and irrigation, and ranged between 45% and 71% of the total fresh weights. In comparison, fruit yield in Lc-1401 and Lp averaged 1.4% and 5.8% of total fresh weight, respectively. La did not produce fruit.

Relative salt tolerance values were calculated on the basis of total shoot and fruit growth of salinized plants compared to the nonsalinized controls (Table 3). When plants are irrigated adequately and when high fruit production of Le is taken into account, the relative salt tolerances of Le, Lc-1401, and Lp to 50 mM solutions are not significantly different. The salt tolerance of La at this treatment was slightly less than the other species. At 100 mM salt, Lp had the highest salt tolerance. The tolerances of the other species at 100 mM were similar to one another and significantly less than that of Lp. Increasing the number of irrigations at this salt concentration improved salt tolerance in all species.

After both 4- and 14-weeks salination in the sand culture study, Le had the highest total fresh and dry weights and La had the least (Table 4). Lc-1401 and Lp were not significantly different in yield from one another at either harvest. Fruit weight of Le increased from 6% to 8% of total fresh weight between 4- and 14-weeks salination. Growth in the wild species was mostly vegetative, and in no instance did fruit weight exceed 14% of the total top fresh weight. Salt had a slight stimulatory effect on the fruit : shoot ratio.

Yields were calculated as total fresh weights of shoots and fruit so that comparisons could be made between Le and the wild species. Salt tolerance curves determined after 4 weeks of salination were similar to those determined after an additional 10 weeks when calculated by either the nonlinear (25) or two-piece linear (12) methods (Fig. 1). Lp and Lc-1401 were more tolerant than Le by virtue of their high threshold values, but yield of Lc-1401 decreased faster as salt concentration increased. As a result of the high productivity of Le, however, actual fresh weights at any of the treatment salt concentrations were not significantly lower than those of any of the wild species. Specific slope, threshold, and tolerance parameters were determined for absolute and relative growth data (Table 2). The relative sensitivity of Le to increasing salt ($Slope_r$) was actually equal to or less than Lp and Lc. La, on the other hand, was significantly less-sensitive to salinity increases, as determined by its low $Slope_r$, than any of the other species. The calculated C_0 value was lower for Le than for the other species.

Leaf and root analysis. Concentrations of the treatment ions, Na^+, Ca^{2+}, and Cl^-, increased with salt treatment in mature leaf tissues in all experiments and in developing leaf and root tissues in the solution culture studies (Fig. 2).

In nonsaline solution cultures, root Na^+ concentrations were significantly higher in Lc-1401 and Lc-1400 than in the other

Table 2. Parameters of salt tolerance response functions of four tomato species calculated on the basis of piecewise linear or curvilinear relationships.

Parameters[z]	Species				
	Le	Lc-1401	Lc-1400	Lp	La
	Vegetative shoot yield in sand cultures				
Threshold	8.14	4.99	0.92[y]	0.92[y]	4.78
	(2.47)[x]	(3.71)	(—)	(—)	(3.66)
$Slope_a$	2.22	3.22	3.64	2.17	1.59
$Slope_r$	5.29	5.70	7.01	4.65	5.04
	(1.20)	(1.67)	(1.72)	(1.18)	(1.42)
r	0.79	0.91	0.75	0.70	0.90
C_0	27.0	22.5	15.2	22.4	24.6
C_{50}	16.4	12.6	4.57	11.2	14.1
	(1.75)	(1.74)	(1.65)	(3.24)	(1.91)
Y_{max}	44.3	57.4	56.6	43.0	31.4
	(3.82)	(6.43)	(6.68)	(5.17)	(3.28)
	Total vegetative and fruit yield in sand cultures				
Threshold	2.74	6.17		7.55	2.76
$Slope_a$	(1.66)[x]	(2.61)		(1.36)	(2.52)
	1.99	1.14		1.36	0.34
$Slope_r$	8.19	9.55		12.26	6.09
	(1.45)	(4.30)		(3.60)	(1.47)
r	0.86	0.87		0.83	0.83
C_0	14.9	19.0		21.4	19.2
C_{50}	7.6	11.3		11.5	10.6
	(1.16)	(1.23)		(0.81)	(0.97)
Y_{max}	24.24	11.95		11.12	5.62
	(2.74)	(1.08)		(0.83)	(0.71)

[z]Threshold = highest salinity in $dS \cdot m^{-1}$ without yield reduction. $Slope_a$ = kilogram fresh weight yield reduction per unit salinity increase above threshold. $Slope_r$ = percentage of yield reduction per unit salinity increase above threshold. r = coefficient of correlation. C_0 and C_{50} salinity in $dS \cdot m^{-1}$ at which calculated yield reaches 0% or 50% of maximum. Y_{max} = maximum theoretical yield in kilograms.

[y]Threshold adjusted to first treatment salinity.

[x]Number of parentheses is SE of the respective mean.

species. Root Na^+ contents increased as salt concentrations increased in the root media, but differences between species were not significant except for the high root Na^+ of Lc-1401 in 50 mM solutions. The overall average root Na^+ increased from 150 to 697 $mmol \cdot kg^{-1}$ dry weight between the 0 and 50 mM salt treatment; however, increasing the salt concentration to 150 mM increased the average root Na^+ to only 794 $mmol \cdot kg^{-1}$, slightly higher than at 50 mM. Increases in Na^+ in the leaves were more in proportion to salinity increases of the root media. Na^+ concentrations in developing leaves of Le under salinity treatments were significantly lower than in similar tissues in other species. Lp and La under saline treatment had consistently higher Na^+ contents than Lc and Le, but these differences were not significant in every case. Na^+ contents in plants grown in sand cultures were similar to those from solution cultures (data not shown).

Root Ca^{2+} averaged over all species increased from 186, in the nonsaline treatment, to 611, 767, and 1032 $mmol \cdot kg^{-1}$ dry weight for the 50-, 100-, and 150-mM salt treatments, respectively (Fig. 2). Lc-1400 had significantly lower root Ca^{2+} concentrations than the other species across salinity treatments. Leaf Ca^{2+} concentrations ranged from 950 to 2480 $mmol \cdot kg^{-1}$ dry weight in mature tissues and from 275 to 1225 $mmol \cdot kg^{-1}$ dry weight in developing tissues.

Root Cl^- averaged over all species increased from 104 $mmol \cdot kg^{-1}$ dry weight for plants grown in nonsaline solutions to 1462, 1812, and 2038 $mmol \cdot kg^{-1}$ dry weight for plants grown

Table 3. The effects of salinity and irrigation frequency on the growth and yield of four tomato species in sand cultures.

Species	Total fresh wt (shoot + fruit) Control (g/plant)	Relative tolerance[z] 50 mM	Relative tolerance[z] 100 mM	Shoot only Control (g/plant)	Relative tolerance 50 mM	Relative tolerance 100 mM
			One daily irrigation			
Le	7730 a[y]	0.96	0.10	4160 b	0.60	0.07
Lc[x]	7620 a	1.09	0.05	7570 a	1.09	0.05
Lp	4350 b	0.78	0.17	4210 b	0.74	0.17
La	2943 c	0.68	0.07	2940 c	0.69	0.07
			Two daily irrigations			
Le	8520 a	0.79	0.13	3770 b	0.52	0.13
Lc	9180 a	0.70	0.14	9150 a	0.70	0.13
Lp	4440 b	0.80	0.31	4250 b	0.76	0.35
La	2690 c	0.51	0.25	2688 c	0.51	0.23

[z]Relative salt tolerance = the yield of saline treated plants divided by the yield of nonsaline control plants.
[y]Means within columns separated by DMRT at $P = 0.05$.
[x]*Lycopersicon cheesmanii*, accession 1401.

Table 4. Growth of four tomato species grown in sand cultures of different salinity for 4 and 14 weeks.

Species	i ($dS \cdot m^{-1}$)	Total fresh wt (kg/plant) 4[y]	Total fresh wt (kg/plant) 14	Dry wt[z] (%) 4	Dry wt[z] (%) 14	Fruit shoot (%) 4	Fruit shoot (%) 14
Le	2.2	2.33	24.2	7.9	10.5	6.3	79.7
	3.6	2.42	22.9	8.1	9.0	5.3	80.2
	5.5	2.11	16.4	7.4	16.1	7.7	82.3
	8.6	1.48	12.8	7.2	13.8	5.2	83.7
	11.8	0.75	4.8	9.4	18.9	9.9	75.4
	13.5	0.86	4.4	10.3	18.8	3.7	76.3
Lc[x]	2.2	1.20	11.3	7.3	16.4	---	3.9
	3.6	1.15	11.2	7.8	14.6	---	2.5
	5.5	1.17	10.9	8.5	10.5	---	2.7
	8.6	0.57	10.0	8.9	11.7	---	5.7
	11.8	0.49	4.7	10.7	15.4	---	6.3
	13.5	0.23	3.5	11.2	15.8	---	9.3
Lp	2.2	1.44	12.1	10.9	13.2	---	11.6
	3.6	1.00	11.9	9.2	12.7	---	7.0
	5.5	0.97	11.8	10.6	12.5	---	4.5
	8.6	0.73	9.0	12.8	14.1	---	14.0
	11.8	0.56	5.7	12.0	14.5	---	10.1
	13.5	0.45	3.3	12.4	14.8	---	6.9
La	2.2	0.56	5.6	10.7	12.4	---	0.1
	3.6	0.69	5.3	11.1	17.7	---	0.3
	5.5	0.64	5.2	10.4	15.4	---	1.2
	8.6	0.71	2.8	11.4	16.9	---	0.6
	11.8	0.46	2.6	12.9	14.9	---	1.5
	13.5	0.45	2.2	13.5	17.9	---	2.4

[z]Percentage of dry weight of vegetative shoot growth.
[y]Weeks under salinization.
[x]1401 ecotype.

in 50-, 100-, and 150-mM solutions, respectively (Fig. 2). Interspecific differences in root Cl^- were not significant.

Typically, K^+ and Mg^{2+} in all leaves decreased as salinity increased, but Mg^{2+} decreased less in developing leaves than in mature leaves. Leaf Mg^{2+} among species ranged from 240 to 360 $mmol \cdot kg^{-1}$ dry weight in mature tissues and between 130 and 220 $mmol \cdot kg^{-1}$ in developing tissues. Mg^{2+} concentrations in mature leaves of Le and Lc-1401 grown in both solution and sand cultures were significantly greater than in the other species. In developing leaves, Mg^{2+} concentrations in La were lower than in the other species. Salt treatments of 50 mM decreased leaf Mg^{2+} by 50% to 65% in mature leaves, but by only about 37% in developing leaves of all species except La. Leaf K^+ concentration was between 1100 and 1400 $mmol \cdot kg^{-1}$

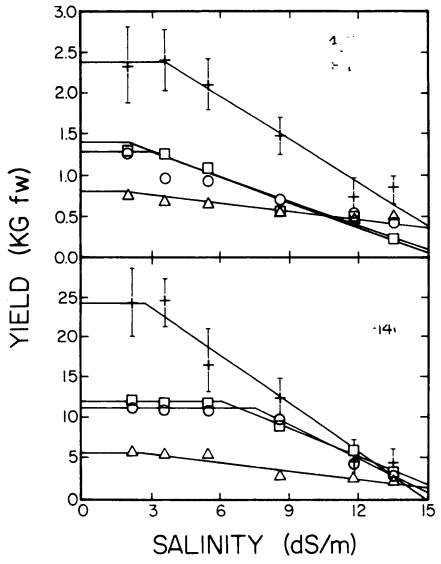

Fig. 1. Salt tolerance of four tomato species grown in sand cultures for 4 weeks (**top**) and 14 weeks (**bottom**) as determined by total vegetative and fruit yields. Nutrient solutions were salinized by 5:1 molar ratio additions of NaCl and $CaCl_2$ to 0, 12.5, 25, 50, 75, and 100 mM total salt concentrations. *L. esculentum* = Le (+), *L. peruvianum* = Lp (○), *L. pennellii* = La (Δ), and *L. cheesmanii*, ecotype 1401 = Lc (□). i = electrical conductivity of the solution in $dS \cdot m^{-1}$; SD = average standard deviations of all species.

dry weight in Le, Lc-1400, and Lp in nutrient solutions without salt; whereas in Lc-1401 and La, leaf K^+ concentrations were about 600 $mmol \cdot kg^{-1}$ dry weight. Initially, a 5% to 20% increase in leaf K^+ with added salt was noted for all species grown in sand culture and for most species (except Lc-1401 and La) grown in nutrient solution. Leaf K^+ was generally lower and changed less in La than in the other species.

Quaternary ammonium compounds were found to consist mostly of choline. Choline concentrations ranged from 46.3 to 30.7 $\mu mol \cdot kg^{-1}$ dry weight in the developing leaves of nonsalinized plants of the different tomato species. Choline concentrations in mature leaves were generally less and ranged from 22.9 to 9.7 $\mu mol \cdot kg^{-1}$. Salinity decreased these concentrations 3% to 30% in most cases. Proline in developing leaves increased as salinity increased in all species (Table 5). Lp and La had the highest leaf proline contents at 0, 50, and 100 mM salt, but Le and Lp had the highest concentrations, around 1 $mmol \cdot kg^{-1}$ fresh weight, at 150 mM salt. Mature leaves did not increase in proline concentration as rapidly in response to salt stress as did the developing leaves. Increases in proline in the mature leaves of Lc-1400 and Lc-1401, in response to 150 mM salt, were barely detectable. Maximum concentrations of proline in Lp and Le at 150 mM salt were only about one-third of those found in developing leaves.

Discussion

Results from solution culture confirm the finding that significant differences in salt tolerance exist between the ecotypes of *L. cheesmanii* (17–19). Differences in shoot and root dry weights between Lc-1400 and Lc-1401 were greatest at 50 mM salinity, a finding that indicates that these species differ in more than their survival at high salinities. These ecotypes were morphologically and developmentally similar but had rather large differences in ion uptake at 50 mM salt. This difference may be

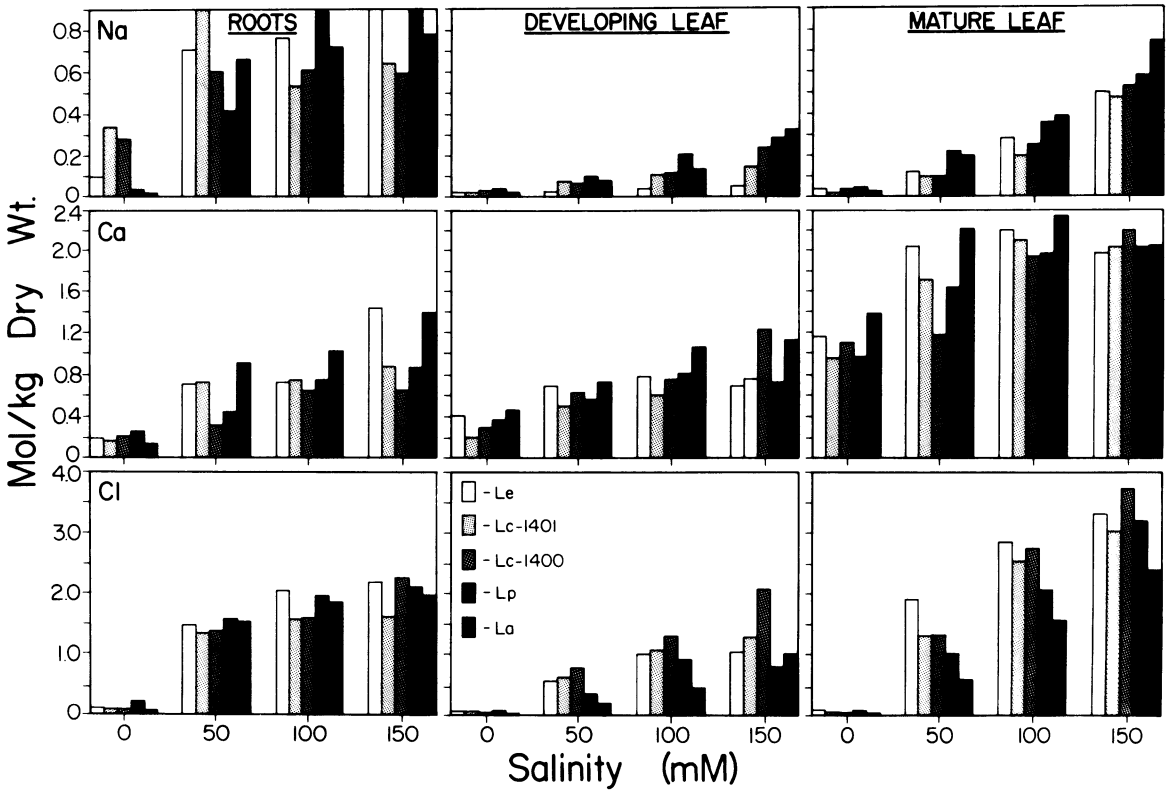

Fig. 2. Sodium, calcium, and chloride contents in roots and developing and mature leaves of four tomato species (*L. esculentum* = Le, *L. peruvianum* = Lp, *L. pennellii* = La, and two ecotypes of *L. cheesmanii* = Lc-1401 and Lc-1400 grown in nonsaline and salinized solution cultures.

Table 5. Leaf free proline concentrations of four tomato species grown in nonsaline and salinized solution cultures.

	μmol proline/g fresh wt							
	Developing leaves				Mature leaves			
Species	0	50	100	150	0	50	100	150
Le	19	82	309	931	24	42	142	337
Lc-1400	53	112	297	518	24	42	19	51
Lc-1401	36	58	171	667	21	45	23	59
Lp	149	258	695	1002	23	125	90	339
La	133	162	395	328	16	15	59	147
$LSD_{0.05}$	81	76	222	323	NS	40	65	85

one component of a wider ranging quantitative salt tolerance character or it may be a specific limiting factor. More studies are needed to determine the answer.

It was surprising to find that the salt tolerance of the cultivated species, Le, was as great, if estimated by the slope, or greater, if estimated by the threshold, than Lc-1401. On the basis of previous studies (18, 19), we had anticipated that Lc-1401 would be more salt-tolerant than the cultivated species. Reasons why our results may differ include salt solution composition, or the possibility that the cultivated variety used as a standard in this study was more salt-tolerant than cultivars used by other investigators. Although the wild tomato species demonstrate substantial variation with respect to many characteristics that may be related to salt tolerance, it should be noted that the variability in many of these characters has not been studied extensively within *L. esculentum* cultivars. Hassan and Desouki (10) found that after 8 weeks salination at 4000 mg·liter^{-1} NaCl, growth reduction among 21 *L. esculentum* cultivars and breeding lines ranged from 12% to 71%.

Plants in sand culture are not exposed to as uniform or constant stress as in solution culture; instead, they undergo wetting cycles that change salt concentrations. Actual field situations, however, involve even more complex ionic, osmotic, and nutritional factors than in sand culture. Thus, in both of these complex environments, the total physiological adjustments that a plant uses to adjust to its environment may include specific mechanisms for osmotic adjustment, ion uptake, or exclusion capacity and drought tolerance that do not come into effect in solution cultures.

In sand culture, Le had one of the lowest salt tolerance thresholds of all species (about 3 dS·m^{-1}), whereas, its threshold in solution cultures was the highest (8.1 dS·m^{-1}). As noted elsewhere, threshold is very sensitive to environmental effects and is difficult to measure without several treatments above and below its anticipated value.

Le was more productive than the wild species at all salinities <15 dS m^{-1} because of its high yield potential (Fig. 1). Previous studies have shown that high-yielding cultivars are more sensitive to stress than cultivars with low yield potential (7, 8). This relationship often is noted in testing cultivars for salt tolerance (22).

Yields of Lc-1401 were as high as those of Le in nonsalinized solution cultures (Table 1) and in sand cultures harvested before extensive fruit production (Table 3). Thus, some of the sensitivity of Le plants grown to maturity may be a result of the effects of salinity on fruit production. Although fruit production is considerably lower in wild species compared to commercial lines, it is maintained or increased under salinity at the expense of vegetative growth.

Dramatic differences among species in Na^+ uptake with increasing salinity may be directly related either to the toxicities of these ions or to their roles in osmotic adjustment. Osmotic adjustment through organic solute synthesis and accumulation may be a key factor in salt tolerance (13). Inositol concentrations in tomatoes increase in response to salt stress. In populations derived from crosses between *L. esculentum* and *L. pennellii*, high *myo*-inositol levels have been correlated with salt tolerance (20). Other studies showed that proline accumulation under salt and osmotic stresses were less in wild tomato species than in the cultivated species (24). Our results for mature leaves support these conclusions; however, developing leaves of the wild species have increased proline levels under nonsaline and low saline (50 mM salt) conditions (Table 5). We have shown that genetic plasticity also exists in proline accumulation among the different tomato species. Whether this accumulation is beneficial to salt tolerance or the result of salt stress cannot be determined by these studies. Proline increases in developing leaves in response to 150 mM salt ranged from 2.5 times in La to about 45 times in Le, and from 2 to 15 times, respectively, in mature leaf tissues (Table 5). Proline has been shown to be a reliable indicator of sensitivity to dehydration associated with flooding stress in tomatoes (1).

In these studies we have demonstrated that there are significant differences between species in both ionic and organic osmotic adjustment. Additionally, salt tolerance may involve specific structural and morphological factors such as shoot : root ratios and ion partitioning mechanisms between developing and mature leaf tissues. Few studies have compared responses between the developing and mature leaf tissues as they relate to salinity and osmotic adjustment, as we have done. Some aspects of salt tolerance may be related to the mechanisms that govern ion content between these tissues.

We found no clear relationship between leaf Na^+, Na : K ratios, or any other character that was measured and salt tolerance. The ability to regulate Na^+, rather than Na^+ content per se, has been more closely correlated with tolerance than any other character (21). The distribution of K^+ and Na^+ in young and mature leaf tissues could be an important part of such regulation. Le was an effective excluder of salt from young leaves and an accumulator in old leaves, K^+ was accumulated in young leaves and was reduced in concentration in more-mature tissues.

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