Breeding Tomatoes for Salt Tolerance: Field Evaluation of *Lycopersicon* Germplasm for Yield and Dry-matter Production

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Abstract. Salt tolerance of 59 cultigens of tomato (*Lycopersicon esculentum* Mill.), seven wild *Lycopersicon* accessions (acc.), and one interspecific hybrid was studied under arid field conditions. Evaluation of salt tolerance was based on relative total dry matter (RD) and relative total yield (RY), calculated as the ratio between performances of saline-treated and control plants. The tomato cultigens were irrigated with water having electrical conductivities (ECi) of 1.5 (control), 5, 10, or 15 dS·m⁻¹. Considerable variation in salt tolerance was found among the cultigens, but at 15 dS·m⁻¹ all showed reduced RD and RY (<0.6). The cultivar M82-1-8 (M82), one accession of *L. cheesmanii* (Lc), three accessions of *L. pennellii* (Lpen), three of *L. peruvianum* (Lper), and an interspecific F₁ hybrid (M82 × Lpen acc. LA-716) were examined for RD at three salinity levels, ECi = 1.5, 10, and 20 dS·m⁻¹, in three annual trials. The salt tolerance of Lpen and Lper were higher than those of M82 and Lc; the interspecific F₁ was the most tolerant and was usually unaffected by even the highest salinity level. The results of this study indicate the existence of a genetic potential for high salt tolerance in wild *Lycopersicon* germplasm.

Salinity is a major factor limiting agricultural production in large areas worldwide. Production under salinity requires technologies for preventing salt accumulation in the soil combined with the use of salt-tolerant crops or cultivars (Epstein et al., 1980; Shannon, 1984; Tal, 1984). As early as 1941, Lyon (1941) suggested that "it may be possible and desirable to select and breed plants for tolerance to saline conditions." There is now considerable research on the genetic approach to the problem (Blum, 1988). To reduce costs and environmental interference involved in replicated field studies, efforts were directed toward development of simpler and quicker systems (Shannon, 1979) and evaluation of traits that characterize salt stress responses (Cruz et al., 1990). Methods have included use of cell cultures and detached organs, evaluation during germination or early seedling stages, and experiments on plants grown in liquid and sand cultures (Jones, 1986; Nieman and Shannon, 1977). However, in spite of intensive research, there are no examples of crop cultivars bred for salinity resistance that have proven to be commercially successful in saline ecosystems (Blum, 1988; Epstein and Rains, 1987).

The cultivated tomato is moderately sensitive to salinity (Maas, 1986). Salinity reduces tomato yield but improves fruit quality traits, such as total soluble solids and acid contents and color (Martinez et al., 1987; Mizrahi et al., 1988). Because of improved fruit characteristics, saline conditions are suitable for the production of high-quality tomatoes for the fresh market and processing.

Relatively high salt tolerance was found in the following wild *Lycopersicon* species: *L. cheesmanii* (Mahmoud et al., 1986;

Rush and Epstein, 1976; Tal and Shannon, 1983), *L. pennellii* (Dehan and Tal, 1978; Shannon et al., 1987; Taleisnik, 1987), and *L. peruvianum* (Shannon et al., 1987). These germplasm resources could be used to breed for salt tolerance in tomato (Rick, 1986); however, the process would be long and labor-intensive.

Our breeding program was designed to develop salt-tolerant tomato cultivars to exploit the large underground reservoir of brackish water available in the Negev desert in Israel (Pasternak, 1982). The approach was based on the assumptions that salt tolerance is an integrated response of various tissues and organs and that breeding for salt tolerance should be addressed to specific environmental conditions. Therefore, the response to salinity was examined at the whole-plant level and under arid field conditions. In this paper, we report the results of field evaluation of salt tolerance in cultivated and wild tomato germplasm over 3 years.

Materials and Methods

Ambient conditions and management. Field trials were conducted during 1984-86 at the Ramat Negev Experimental Station in the Negev desert in Israel. The climate at this location is arid, with an average annual winter rainfall of 100 mm. Monthly mean temperatures ranged from 10C in April to 20C in August (minimum) and from 25 to 34C (maximum). Pan evaporation ranged from 7 to 11 mm·day⁻¹. The sandy loam soil was uniform to a depth of 90 cm or more and contained 60% to 70% sand, 15% to 20% clay, and 10% to 15% loam, with a volumetric field capacity of 14% to 15%.

For 3 years before each trial, wheat was grown in the experimental plots and was sprinkler-irrigated with fresh water to ensure a uniform and leached soil. Plot preparation included plowing; applying 4 t manure/ha (2.5% N, 2.5% P₂O₅, 2.4% K₂O, 55% organic matter), 100 kg N/ha, 110 kg P/ha, and 250

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Abbreviations: acc., accessions; ECe, electrical conductivity of saturated soil extract; ECi, electrical conductivity of irrigation water; Lc, *Lycopersicon cheesmanii*; Le, *Lycopersicon esculentum*; Lpen, *Lycopersicon pennellii*; Lper, *Lycopersicon peruvianum*; RD, relative total dry matter; RY, relative total yield.

kg K/ha; and bed formation. Additional N (250 kg·ha⁻¹) and P (70 kg·ha⁻¹) were applied with the irrigation water.

Since previous experiments with tomatoes indicated seedling establishment to be the stage most sensitive to salt (Pasternak et al., 1986), fresh water was applied until anthesis of the first flowers (3 to 4 weeks after transplanting), after which saline water was introduced. Water was applied three times a week by a drip system with drippers spaced 50 cm apart. All plots received the same quantity of water, according to the water requirement of the control. This amount was higher than that required for the saline treatments and thus included some excess water for leaching. The amount of water per application was based on 'Class A' pan evaporation (40% to 100% of the evaporation, varying with developmental stage). A total of 400 to 490 mm of water was applied per season; in the saline plots, 85% to 90% of the water was saline. Salinity levels were determined according to the EC_i of the irrigation water. Artificial saline water was produced by mixing a concentrated salt solution with fresh water (EC_i = 1.5 dS·m⁻¹). The salts used were NaCl and CaCl₂ at a molar ratio of 4:1, similar to that of the local aquifer. The actual EC_i varied by not more than 5% from the desired value. To achieve a uniform and controlled salinization, plants were spaced 50 cm apart and grown 5 to 10 cm from the dripper locations. A single row was planted on each 1.96-m-wide bed (one plant/m²) with a single drip line, or alternatively, two rows were planted 60 cm apart (two plants/m²) with two drip lines.

Soil salinity was monitored two to three times a season, from 20 days after the start of salinization until harvest. Soil was sampled from depths of 0 to 30 cm and 30 to 60 cm at the planting location; the electrical conductivity of the saturated soil extract (EC_e) was determined with a conductometer (CDM83; Radiometer, Copenhagen).

Tomato cultigens. Fifty-nine tomato cultivars and breeding lines (listed in Table 4; denoted hereafter as cultigens), considered to represent a diverse genetic background, were examined for salt tolerance. Water at EC_i = 1.5 (control), 5, 10, or 15 dS·m⁻¹ was applied in split plots (salinity in main plots) with nine replications and a single plant per subplot. Plants were directly seeded on 12 May 1985 and thinned after emergence to a stand of one plant/m². Harvest at fruit ripening began on 18 Aug. 1985.

Lycopersicon species. Seven wild acc. of Lpen, Lper, and Lc, a control *L. esculentum* (Le) cultivar, and an interspecific hybrid (Le × Lpen) were examined over 1 to 3 years as specified in Table 1.

Water at EC_i = 1.5 (control), 10, or 20 dS·m⁻¹ was applied using a split-plot design (salinity in main plots). The 1984 experiment consisted of two replications and five plants per subplot. Seedlings (one plant/m²) were transplanted on 3 Apr. and

harvest began on 20 June at the fruit ripening stage of M82. The 1985 experiment was similar to that of the previous year, but with double the plant density (two plants/m²) and earlier harvest. Plants were transplanted on 26 Apr. and harvested at the fruit set stage, starting on 23 June. The 1986 experiment consisted of six replications with one plant per subplot. Plants (one plant/m²) were transplanted on 13 Apr. and harvested at the fruit ripening stage of M82 on 1 July.

Dry matter and yield. Each plant was cut at the soil surface, and vegetative (leaves and stems) and reproductive (fruit) fractions were separated and weighed and samples (300–500 g) taken from each. The vegetative sample included one or two branches with mature and young parts. Samples were placed in plastic bags and kept at 4°C for up to 2 days, at which time the vegetative sample was separated into leaves and stems and the fruits were cut into pieces. All the plant fractions were oven-dried (80°C for 48 to 72 h) and the dry matter percentage of each was determined. The total dry matter was calculated from fresh weights × dry weight percentages of the samples. RY and RD were calculated as the ratio between fresh fruit yield or total dry matter per plant of each plot (excluding nonsurviving plants) and the respective average values for the same genotypes under control conditions. RY was not measured for the wild species since in many cases self-incompatibility prevented fruit set.

Statistics. Data were tested by analysis of variance (ANOVA) and means were separated at *P* = 0.05 by the Student–Newman–Keul's multiple range test.

Salinity response function of M82 to EC_e was established according to the model suggested by Maas and Hoffman (1977). This was calculated by a linear regression analysis of RD or RY on EC_e based on treatment means from all experiments, excluding controls. Other cultigens, for which data were not sufficient for such an analysis, were classified according to "highest tolerable treatment," i.e., the highest EC_i at which RD was above 0.8, a value considered to indicate a substantially reduced growth.

Results and Discussion

Soil salinity. Soil salinity was uniform during the saline irrigation period within the upper 60 cm of soil. EC_e under control conditions was 2.3 dS·m⁻¹ (mean of the four experiments; Table 2), a value reported to be within the range tolerable by tomato plants without yield reduction (Maas, 1986), as also confirmed for our control cultivar (see below). The EC_e was usually about half of the EC_i for the salinity treatments. At field capacity (i.e., about half water content of saturation), the EC_e was similar to EC_i, indicating that the soil salinity was stable and the leaching was sufficient to prevent salt accumulation.

Table 2. EC_e as affected by EC_i.

EC _i (dS·m ⁻¹)	EC _e ± SE (dS·m ⁻¹)			
	Tomato cultigens	Lycopersicon species		
	1985	1984	1985	1986
1.5 ^y	2.0 ± 0.1	2.5 ± 0.3	1.6 ± 0.2	3.1 ± 0.4
5	3.7 ± 0.3			
10	6.8 ± 0.5	5.9 ± 0.5	5.3 ± 0.4	5.3 ± 0.4
15	10.3 ± 0.5			
20		9.3 ± 0.7	8.9 ± 0.8	7.9 ± 0.5

^yEC_e values were averaged over the upper 60 cm of soil and over the entire salinization period.

^yFresh-water control.

Table 1. Acc. examined in three *Lycopersicon* species trials.

Species and genotype	Symbol	Year of evaluation		
		1984	1985	1986
Le cultivar M82-1-8	M82	+	+	+
Lpen acc. LA-716	Lpen716	+	+	+
F ₁ (M82 × Lpen716)	F ₁	+	+	+
Lc acc. LA-1401	Lc1401	+	+	
Lpen acc. LA-1657	Lpen1657	+	+	
Lper acc. PI-127831	Lper127831	+	+	
Lper acc. PI-127832	Lper127832		+	
Lper acc. PI-111	Lper111		+	
Lpen acc. LA-1941	Lpen1941		+	

The response curve of M82, a control cultivar. The mean absolute yield of the control cultivar M82 obtained with 1.5 dS·m⁻¹ was 6 kg/plant over the three growing seasons (when examined with both the tomato cultigens and the wild species). This value is within the range expected under proper agricultural practices.

The response functions of M82 to soil salinity in terms of RY and RD were similar and both significant at $P = 0.05$ (Table 3). An increase of 1 dS·m⁻¹ in ECe above the threshold of 2 to 2.5 dS·m⁻¹ resulted in a 9% to 10% reduction in RY and RD. The salinity response curves of M82 were similar to those previously reported for tomato (Maas, 1986).

Tomato cultigens. The highest tolerable salinity (RD > 0.8) was 1.5 dS·m⁻¹ for 11 cultigens, 5 dS·m⁻¹ for 31 cultigens, and 10 dS·m⁻¹ for 17 cultigens (Table 4). No cultigen tolerated the 15 dS·m⁻¹ treatment, where the maximum RD values were 0.6. The control cultivar, M82, was moderately sensitive, as were most of the cultigens evaluated. RD was highly correlated with RY ($R^2 = 0.93$, $n = 988$).

The average plant survival rates were 0.94, 0.88, 0.76, and 0.24 at salinity levels of ECi = 1.5, 5, 10, and 15 dS·m⁻¹, respectively. At 15 dS·m⁻¹, maximum survival rate was 0.55. Plant survival was not associated with the highest tolerable treatment.

Four selected cultigens, M82, FAR-77-247-1 (F77), Bulgaria 12 (B12), and Mercado (MER), with a range of salinity responses (Fig. 1), had absolute yields of 4.9 to 6.2 kg/plant under control conditions. In F77 and M82, for which the highest tolerable treatments were 1.5 and 5 dS·m⁻¹, respectively, RD and RY were significantly reduced by salinity. No significant effect of salinity was observed in B12 and MER, with the highest tolerable salinity having been 10 dS·m⁻¹.

The considerable variation found among the Le cultigens in their response to salinity (Table 4, Fig. 1) indicates that it should be possible to select tolerant cultivars for production under saline conditions with fresh water applied only for plant establishment. Of the 14 indeterminate cultigens, eight were in the tolerant group (highest tolerable treatment 15 dS·m⁻¹). This grouping may indicate an influence of the growth habit on the response to salinity. Average harvest indices (reproductive : total dry matter ratio) in the control were 0.54, 0.47, and 0.44 for the sensitive, moderate, and tolerant cultigen groups, respectively, with no appreciable change under salinity. Average yields of these cultigen groups were 5.0, 4.6, and 4.1 Kg/plant in the control, and 2.2, 2.5, and 3.7 Kg/plant under the 10-dS·m⁻¹ treatment, respectively. As tolerance increases, productivity appears to decrease in terms of harvest index and yield under fresh-water irrigation. However, in terms of yield and relative yield under salinity, productivity increases with increas-

Table 3. Response functions of RD and RY of Le 'M82-1-8' to soil salinity.

No. trials	Dependent variable	R^2	df	Function ^a	
				Threshold (ECe = dS·m ⁻¹)	Slope ^b (% per dS·m ⁻¹)
4	RD	0.59	8	2.5	-9.2
3 ^c	RY	0.78	6	2.0	-9.9

^aCalculated according to the model of Maas and Hoffman (1977), based on treatment means.

^bExpresses the reduction in RD or RY in response to an increase in ECe above the sensitivity threshold.

^cThe 1985 *Lycopersicon* species trial was not included because the plants were harvested before fruit ripening.

Table 4. Highest tolerable treatment^a of 59 tomato (*L. esculentum*) cultivars or breeding lines.^b

ECi = 1.5 dS·m ⁻¹	ECi = 5 dS·m ⁻¹	ECi = 10 dS·m ⁻¹
(P) FAR-77-247-1	(P) Castle Long	(ID) Alcobaca
(D) L22	(P) Castle Rock	(D) Arava
(D) N4-F4-210-2	(P) E-6203	(ID) Bornia
(P) Peto-86	(P) FAR-81-127	(ID) Bulgaria 12
(P) Peto-95	(P) FAR-84-267	(ID) FA-19
(D) R5	(P) FAR-300	(ID) FA-111
(D) R8	(D) Gali	(D) Floradade
(D) R13	(D) High Sugar	(ID) Mercado
(P) UCX-142-1-2	(P) Hofit	(D) MK-677
(P) Vis	(ID) Marmande VFN	(D) N4-F4-210-1
(ID) 760-G	(D) MK-2	(ID) Potentate
	(ID) MK-216	(D) Saverianin
	(D) MK-606	(ID) Scorpio
	(P) M82-1-8	(P) S-80-262-4
	(D) Na'ama	(P) VF-134-1-2
	(D) N4-F4-222-1	(P) VF-211
	(D) RN-80-5-10	(P) 97-3
	(D) RN-80-5-20	
	(P) RS-1300 VF	
	(ID) R2	
	(ID) R3	
	(D) R4	
	(D) R6	
	(D) R10	
	(D) R11	
	(D) R12	
	(D) Saturn	
	(P) S-80-285-1	
	(ID) Tropic	
	(D) T-6	
	(P) VF-145	

^aThe highest salinity treatment at which RD > 0.8.

^bCultigen types are indicated in brackets as: determinate (D) or indeterminate (ID) fresh-market tomatoes or determinate tomatoes for processing (P).

Fig. 1. Effect of saline water irrigation on RD (A) and RY (B) of four tomato cultivars: M82-1-8 (M82), FAR-77-247-1 (F77), Bulgaria 12 (B12), and Mercado (MER). Significant interactions (salinity × cultigen) were found for both measurements. Mean separation by Student-Newman-Keuls's multiple range test, between treatments within each cultigen (a, b), at $P = 0.05$. Means having the same letter, or having no letter, are not different.

ing tolerance, which is an important factor from the practical point of view.

***Lycopersicon* species.** Salt tolerance in the wild *Lycopersicon* species was examined over 3 years on the basis of RD. The absolute total dry matter under control conditions was 1.8 kg/plant for the F₁ and ranged from 0.45 to 0.7 kg/plant for the other genotypes. In 1984, the F₁ had the highest RD at both 10 and 20 dS·m⁻¹ (Fig. 2); however, it differed significantly only from M82 and Lc1401. A stronger salinity effect was observed in 1985: two of the Lper lines had the highest RD at 10 dS·m⁻¹, while at 20 dS·m⁻¹, the F₁ showed the lowest reduction in dry matter. In 1986, RD was not significantly affected by either salinity or genotype; however, in M82 and Lpen716, RD was reduced by salinity. ECI of the control was relatively high in 1986 (Table 2), which may have reduced the total dry matter in the control and thus increased the RD under the salinity treatments.

Salt tolerance was higher in Lpen and Lper than in the cultivated tomato or Lc (Fig. 2). The F₁ showed hybrid vigor and was found to be the most tolerant genotype in all three annual trials; in two of the trials it was unaffected by the salinity treatments. Some of these differences between species in salt tolerance may be a result of the different growth habits and fruit productivity. Variations for a particular genotype over years indicate the necessity of testing the material over time.

Our results agree with previous reports of high salt tolerance in Lpen (Dehan and Tal, 1978; Shannon et al., 1987; Taleisnik,

1987) and Lper (Shannon et al., 1987), which originate from arid regions of South America (Taylor, 1986). Lc was found in the Galapagos Islands near the high tide line (Rick, 1973) and would be expected to have high salinity tolerance. This expectation was borne out by several nutrient culture experiments in the greenhouse (Mahmoud et al., 1986; Rush and Epstein, 1976; Tal and Shannon, 1983). In contrast to these results, Lc in our experiments was the most sensitive of the three wild species and responded similarly to the control cultivar (Fig. 1). A similar finding was obtained by Shannon et al. (1987) in outdoor sand culture plots. The contradictory results may stem from environmental differences between nutrient culture in greenhouse and outdoor experiments.

The response to salinity of the cultivated tomato and of the wild species were examined in different trials, thus limiting the possibility of comparison between them. Similar ECE values were obtained in the 15-dS·m⁻¹ treatment of tomato cultigens in 1985 and in the 20-dS·m⁻¹ treatment of wild *Lycopersicon* species in 1984 and 1985 (Table 2). Under these similar conditions, the tolerant cultigens had RD values below 0.6 and survival rates below 0.55, while the tolerant wild accessions had RD values similar to those of the tolerant cultigens, and the F₁ had an average RD of 0.8. Few of the wild species or F₁ plants died. Our results indicate that Lpen and Lper have a higher genetic potential for salt tolerance than Le cultigens.

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Fig. 2. Effect of saline water irrigation on RD of Le 'M82-1-8' (M82), Lpen, Lc, and Lper (abbreviated species names are followed by acc. number), and an interspecific F₁ (M82 × Lpen716). Significant effect of genotypes was found in 1984, significant effect of salinity in 1985, and no significant effect in 1986. Mean separation between genotypes as a main effect (a, b) by Student-Newman-Keuls's multiple range test at $P = 0.05$. Means having the same letter, or having no letter, are not different.

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