Salinity Tolerance in Four Wild Tomato Species using Vegetative Yield-Salinity Response Curves

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Additional index words. *Lycopersicon pimpinellifolium*, *L. peruvianum*, *L. hirsutum*, *L. pennellii*, nutrient solution, Na⁺ ion, Cl⁻ ion

Abstract. The salinity tolerances of 21 accessions belonging to four wild tomato species [*Lycopersicon pimpinellifolium* (Jusl.) Mill., *L. peruvianum* (Corr.) D'Arcy, *L. hirsutum* (L.) Mill., and *L. pennellii* Humb. Bonpl.] were evaluated using their vegetative yield-salinity response curves at the adult stage, determined by a piecewise-linear response model. The slope (yield decrease per unit salinity increase), salinity response threshold, maximum electrical conductivity without yield reduction (EC₀), and salinity level for which yield would be zero (EC₀) were determined by a nonlinear least-squares inversion method from curves based on the response of leaf and stem dry weights to substrate EC. The genotype PE-2 (*L. pimpinellifolium*) had the highest salt tolerance, followed by PE-45 (*L. pennellii*), PE-34, PE-43 (*L. hirsutum*), and PE-16 (*L. peruvianum*). The model also was tested replacing substrate salinity levels with leaf Cl⁻ or Na⁺ concentrations. Concentrations of both ions for which vegetative yields were zero (Cl₀ and Na₀) were determined from the response curves. In general, the most tolerant genotypes were those with the highest Cl₀ and Na₀ values, suggesting that the dominant salt-tolerance mechanism is ion accumulation, but there were cases in which salt tolerance was not related to Cl₀ and Na₀.

Investigation of salt tolerance potential *Lycopersicon* and its closely related wild species was initiated by Lyon (1949), who suggested that salt tolerance might be improved by introgressing genes from *Lycopersicon pimpinellifolium* to the cultivated tomato. High salt tolerance has been reported for other wild relatives of the cultivated tomato (Dehan and Tal, 1978; Phills et al., 1979; Rush and Epstein, 1976; Tal, 1971). As these wild species (*L. cheesmanii*, *L. peruvianum*, *L. pennellii*, *L. hirsutum*, etc.) can be crossed with more or less difficulty to the cultivated tomato, they represent potential gene sources of salt tolerance that could be exploited by interspecific hybridization. Wide differences in salinity tolerance have been found between and within wild species (Shannon et al., 1987). Therefore, before beginning a breeding program, it would be useful to screen genotypes suitable as parents for developing salinity-tolerant lines.

Salt tolerance of crop plants usually has been expressed as the yield decrease for a given level of soluble salts in the root medium compared with yields under nonsaline conditions (Bernstein et al., 1974). Maas and Hoffman (1977) expressed salinity tolerance of agricultural crops by two characteristics: salinity threshold (the maximum level of salinity that can be tolerated without loss of yield) and slope. Slope was calculated by linear regression of yield decrease vs. salinity level increase beyond the threshold. Feinerman et al. (1982) proposed a more accurate switching regression method to estimate the coefficients of the piecewise linear response model. Unfortunately, their method was restricted to those data sets that had at least two data points to the left and at least three points to the right of the fitted threshold value. This restriction makes the method less suitable for experiments with relatively few data points than

for those with many data points. Further, van Genuchten (1983) used a more general nonlinear least-squares method to simultaneously estimate the three unknown characteristics, maximum yield, slope, and salinity threshold, of the three piecewise linear salt-tolerance response functions. The yield-salinity response model has been applied not only to fruit yield but also to development features, such as height (Anastasio et al., 1987) and vegetative yield (Shannon et al., 1987). However, the substrate salinity level has been expressed in terms of electrical conductivity of the substrate or in terms of leaf concentration of salt stress inductor ions (Bingham et al., 1985).

In our work, the model proposed by van Genuchten (1983) was used to evaluate the salinity tolerance of 21 genotypes belonging to four *Lycopersicon* wild species and to select those that could be used as parents in breeding programs. Salinity tolerance cannot be assessed by fruit yield since the *L. peruvianum*, *L. hirsutum*, and *L. pennellii* entries are not always self-compatible. Therefore, the model was applied to two attributes of vegetative yield; i.e., leaf and stem dry weights vs. substrate salinity levels. The model also has been applied in this work using leaf Cl⁻ and Na⁺ concentrations instead of substrate salinity levels.

Materials and Methods

The 21 genotypes (Table 1) were chosen because their salinity tolerance had not been evaluated previously and because *L. pimpinellifolium*, *L. peruvianum*, and *L. pennellii* had been described as potential sources for salt tolerance (Lyon, 1941; Shannon et al., 1987). *L. hirsutum* salt tolerance was unknown at the mature stage.

Seeds of the wild species were soaked in 2.7% (v/v) NaOCl for 45 min and rinsed thoroughly with distilled water before germination (Tal and Shannon, 1983). Seeds were germinated

Received for publication 4 June 1990. This research has been supported by CAICYT (Project no. PA-85/140). 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.

Abbreviations: EC, electrical conductivity; LDW, leaf dry weight; SDW, stem dry weight.

Table 1. Components of salt tolerance response curves of four wild tomato species calculated on the basis of piecewise linear model.

Species ^y and accession	Leaf dry wt (g)			Stem dry wt (g)		
	EC ₀ ^z (S·m ⁻¹)	Cl ₀ (mg·g ⁻¹)	Na ₀ (mg·g ⁻¹)	EC ₀ (S·m ⁻¹)	Cl ₀ (mg·g ⁻¹)	Na ₀ (mg·g ⁻¹)
<i>L. pim.</i>						
PE-2	6.72	363.5	202.5	5.76	346.2	199.1
PE-8	2.57	104.6	64.5	2.57	97.5	61.5
PE-13	3.12	85.3	44.6	2.71	75.7	39.4
PE-14	2.56	96.9	64.5	2.85	104.0	67.2
PE-15	2.62	84.4	55.1	2.57	83.5	54.4
<i>L. per.</i>						
PE-16	3.38	93.2	24.3	2.89	78.1	21.6
PE-18	2.19	92.8	27.2	2.46	95.7	43.8
PE-20	1.55	37.0	18.7	2.57	107.5	35.8
PE-51	2.26	87.2	24.7	2.51	119.1	25.2
PE-52	1.63	81.4	---	1.63	94.8	26.4
PI-40	2.95	137.5	77.5	2.46	92.4	63.7
PI-48	2.42	110.9	62.1	2.36	108.0	58.9
<i>L. hir.</i>						
PE-34	3.55	262.1	115.0	2.56	118.5	62.7
PE-35	2.15	49.3	31.6	2.29	47.3	30.5
PE-36	2.89	72.4	34.7	2.36	70.4	23.9
PE-37	2.97	86.9	54.0	2.21	60.9	42.5
PE-39	2.39	48.9	26.1	2.36	55.8	33.1
PE-41	3.12	85.4	48.2	2.71	63.9	39.0
PE-43	3.43	96.7	51.4	3.43	110.1	58.2
<i>L. pen.</i>						
PE-45	3.15	306.1	173.0	2.62	158.5	96.5
PE-47	2.69	---	---	2.76	---	---
LSD _{0.05}	0.38	17.5	4.3	0.32	9.9	3.5

^zEC₀, Cl₀, and Na₀ = EC of the substrate, and Cl⁻ and Na⁺ leaf concentrations at which LDW and SDW would reach zero.

^y*L. pim.* = *Lycopersicon pimpinellifolium*; *L. per.* = *L. peruvianum*; *L. hir.* = *L. hirsutum*; *L. pen.* = *L. pennellii*; PI-40 = PI-126440; PI-48 = PI-126448.

in darkness on filter paper soaked with distilled water, and, after emergence, seedlings were transferred to rock wool as a culture substrate in the greenhouse. Seedlings were irrigated with a nutrient solution containing (in mM): 1.72 K₂SO₄, 5.44 KNO₃, 3.05 Ca(NO₃)₂, 0.5 NH₄NO₃, 1.35 HNO₃, 1.81 H₃PO₄, and (in μM) 75.1 Fe as diethylene-triamine pentaacetate, 16.70 H₃BO₃, 1.38 ZnSO₄, 1.10 CuSO₄, 0.52 Na₂MoO₄, and 16.4 MnSO₄.

Control plants were irrigated with the nutrient solution, and treated plants with nutrient solution plus NaCl at 2, 4, or 8 g·liter⁻¹ from the time that plants had five true leaves until the end of experiment. The rock wool substrate underwent rapid salinization until equilibrium of the substrate with the irrigation solution was reached (7 days). The average root-zone ECs were measured on the lixiviated solutions 60 min after irrigation was started. The EC of the substrate irrigated with nutrient solution was 0.28 S·m⁻¹ and the ECs of the substrates irrigated with NaCl (2, 4, and 8 g·liter⁻¹) were 0.63, 1.39, and 2.15 S·m⁻¹, respectively. The initial pH values of the nutrient solution and the three saline solutions were 6.9, 6.8, 6.4, and 6.4, respectively, although they were maintained between 6.0 and 6.5 with additions of H₂SO₄. Daily mean maxima and minima in the greenhouse were 37 ± 2C and 22 ± 1C, respectively.

The experiment was conducted in three blocks, and in each block, three plants per genotype and treatment were analyzed. The plants were harvested 10 weeks after the beginning of saline treatments. LDW and SDW were determined and leaf samples were taken for chemical analysis for each plant. Leaf tissue was analyzed for Cl and Na concentrations. Chloride was deter-

mined by potentiometric titration with AgNO₃ (Johnson et al., 1958). Sodium was measured by emission spectrophotometry of a 2 nitric : 1 perchloric digestion extract.

The model proposed by van Genuchten (1983) for evaluating crop salt tolerance was used to determine the response curves of LDW and SDW to the EC of the substrate or to leaf Cl⁻ and Na⁺ concentrations. The replacement of substrate EC by Cl⁻ or Na⁺ leaf concentrations was supported by the linear relationship between substrate Cl⁻ and Na⁺ concentrations and the absorption of these ions by the plant, as shown by Rush and Epstein (1976) and by us (data not shown).

The model is given by:

$$Y = \begin{cases} Y_m & 0 \leq EC \leq EC_t \\ Y_m - Y_m \cdot s(EC - EC_t) & EC_t < EC \leq EC_o \\ 0 & EC > EC_o \end{cases}$$

where Y = absolute yield, Y_m = theoretical maximum yield, Y_m·s = slope (yield decrease per unit salinity increase), EC = electrical conductivity of root medium solution, EC_t = EC threshold (maximum salinity without yield reduction), and EC_o = EC at which yield would reach zero. The computer "SALT" program (van Genuchten, 1983) was used to determine simultaneously Y_m, slope, EC_t, and EC_o. We selected option 5, as it allows no *a priori* fixing of any condition (neither the points to the left nor to the right of threshold, nor maximum yield) and simultaneously computes the parameters using Marquardt's approximation algorithm (Marquardt, 1963). As a criterion for goodness-of-fit of the data to the theoretical model, the coeffi-

cient of determination (R^2) was used. Absolute values must be used for this model. The response functions were determined for the three blocks together and for each block individually to verify the influence of blocks. For each genotype, standard deviations of the Y_m and slope calculated values for each block were determined. Analysis of variance was performed for EC_o and leaf Cl (Cl_o) and Na (Na_o) concentrations, at which LDW and SDW would reach zero. Significant differences among genotypes were determined by the LSD values.

Results

Salinity threshold and slope values. Salinity reduced LDW and SDW for all genotypes of the four *Lycopersicon* species, and the data fit the model well. Most R^2 values were higher than 0.70 (Fig. 1).

Among the five accessions of *L. pimpinellifolium*, Y_m ranged from 201 to 351 g for LDW and from 138 to 336 g for SDW (Fig. 1). Both dry weights decreased with increasing salinity. For this reason, their tolerance cannot be assessed on the basis of a salinity threshold. Based on slope values, PE-2 would be the most salt-tolerant genotype, as it had the lowest slope value, PE-13 was the second most salt-tolerant of the *L. pimpinellifolium* genotypes, followed by PE-15, PE-14, and PE-8, which was the most salt-sensitive. In relation to the control plants, LDW and SDW of PE-2 were reduced by 30% and 37%, respectively, at the highest salinity level, while PE-8 had a decrease of 85% and 75%. PE-14 was the only genotype of *L. pimpinellifolium* showing significant differences in slope between LDW and SDW. LDW salt tolerance of PE-14 was similar to that of PE-8, but SDW salt tolerance of PE-14 was higher than PE-8 and similar to PE-15.

Some accessions of *L. peruvianum* had a low threshold value for SDW, but all values were $<0.28 \text{ S}\cdot\text{m}^{-1}$ (Fig. 2). Thus, the threshold salinity cannot be used to evaluate the salinity tolerance of the *L. peruvianum* genotypes. Based on slope, PE-16 was the most salt-tolerant. This genotype, which had the lowest LDW and SDW values at low NaCl concentrations, was one of the highest yielding at the highest salinity level tested, and its LDW and SDW reductions compared to the control plants were of 63% and 73%, respectively. PI-40 was the second most salt-

Fig. 1. Vegetative yield-electrical conductivity response curves of five genotypes from *L. pimpinellifolium*. Y_m = maximum theoretical dry weight. Slope = dry weight reduction per unit salinity increase. R^2 = coefficient of determination. Numbers in parentheses are standard deviations of the respective means.

Fig. 2. Vegetative yield-electrical conductivity response curves of seven genotypes from *L. peruvianum*. Y_m = maximum theoretical dry weight. Slope = dry weight reduction per unit salinity increase. R^2 = coefficient of determination. Numbers in parentheses are standard deviations of the respective means.

Fig. 3. Vegetative yield-electrical conductivity response curves of seven genotypes from *L. hirsutum*. Y_m = maximum theoretical dry weight. Slope = dry weight reduction per unit salinity increase. R^2 = coefficient of determination. Numbers in parentheses are standard deviations of the respective means.

tolerant of the *L. peruvianum* genotypes. PE-52 had zero dry matter yield at $1.7 \text{ S}\cdot\text{m}^{-1}$ and was the least salt-tolerant accession. PE-20 and PE-18 changed their behavior when LDW and SDW were considered. PE-20 had the steepest slope for LDW and an intermediate one for SDW. PE-18 slope was intermediate for LDW and highest for SDW.

Dry weight yields of leaves and stems for *L. hirsutum* entries were from 274 to 666 g (Fig. 3). *L. hirsutum* had the highest yield among the four species groups. However, some of the entries would have zero dry matter yield at $2.15 \text{ S}\cdot\text{m}^{-1}$ salinity level. Based on slope values, PE-35 and PE-39 were the most salt-sensitive of the *L. hirsutum* genotypes (295 and 259 g LDW decrease, respectively, per unit of increase of the substrate EC). The entries PE-34, PE-36, and PE-43 had the shallowest slope, around 115 g yield decrease per unit increase in salinity level. PE-37 was one of the best genotypes when LDW was considered and it had one of the steepest slopes according to stem dry

Fig. 4. Vegetative yield-electrical conductivity response curves of two genotypes from *L. pennellii*. Y_m = maximum theoretical dry weight. Slope = dry weight reduction per unit salinity increase. R^2 = coefficient of determination. Numbers in parentheses are standard deviations of the respective means.

weight, but this was the only *L. hirsutum* accession changing its behavior.

The two entries of *L. pennellii* were not significantly different in salinity tolerance (Fig. 4). The slopes were of the same order as those of the most salt-tolerant *L. hirsutum* genotypes although their maximum LDWs were lower.

EC_o , Cl_o , and Na_o values. The salinity beyond which the yield becomes zero, EC_o , was calculated according to the equation: $EC_o = EC_i + Y_m \cdot \text{slope}^{-1}$.

EC_o is defined by both slope and threshold parameters; consequently, this parameter could be more useful for evaluating the salinity response of genotypes. According to EC_o values determined by the function vegetative yield vs. EC, PE-2 was the most salt-tolerant genotype of *L. pimpinellifolium*, PE-16 and PI-40 of *L. peruvianum*, and PE-34 and PE-43 of *L. hirsutum* (Table 1). These results were similar to the ones obtained from the slope values. Thus, the slope values had more influence on EC_o than Y_m and threshold values.

The model not only was applied according to the substrate salinity level, but also according to Cl^- and Na^+ leaf concentrations. Cl_o and Na_o parameters were determined for all the genotypes whose data fit the model. Cl_o and Na_o gave almost identical results because both resulted in three groups in *L. pimpinellifolium*: PE-2, PE-8 and PE-14, PE-13 and PE-15 (Table 1). Results of Cl_o and Na_o also coincide for *L. peruvianum* and *L. hirsutum*. When the highest values are considered, PI-40 and PI-48 were the most salt-tolerant *L. peruvianum* genotypes and PE-34 and PE-43 were for *L. hirsutum* genotypes.

The most important difference between the calculated EC_o values and those of Cl_o and Na_o was that PE-16 did not accumulate as much Cl^- and Na^+ in the leaves and stems as did most of the other genotypes.

Na_o : Cl_o ratios were lower in *L. peruvianum* than in other species, with the exception of PI-40 and PI-48, which belong to *L. peruvianum glandulosum*.

Considering the four species together, PE-2, PE-43, and PE-16 had the highest EC_o values for LDW and SDW; PE-2, PE-45, PE-34, and PI-40 were the accessions with highest Cl_o values for LDW; and PE-2, PE-45, PE-34, PE-51, and PE-43 for SDW. The most tolerant genotypes based on Na_o for LDW and SDW were PE-2, PE-45, PE-34, PI-40, and PE-14.

Discussion

The wild relatives of the cultivated tomato represent a potential source of useful genetic variation (Rick, 1988). Variation

for salt tolerance has been previously demonstrated within *L. peruvianum* and *L. pennellii* (Dehan and Tal, 1978; Tal, 1971; Tal and Shannon, 1983). However, the *L. pimpinellifolium* and *L. hirsutum* species have been the least tested in plant breeding. Jones (1986) included two entries from *L. pimpinellifolium* and one from *L. hirsutum* when assessing the salinity tolerance of different tomato species at the germination stage. In this work, besides *L. peruvianum* and *L. pennellii*, *L. pimpinellifolium* and *L. hirsutum* also were tested for salinity tolerance.

In the four wild species of *Lycopersicon*, even the lowest salt concentration decreased the LDW and SDW. For this reason, their tolerance cannot be assessed on the basis of the salinity threshold, but on the basis of the slope of the function vegetative yield vs. EC.

Genotype salt tolerance evaluation by slope and EC_o gave similar results using either LDW and SDW, except for three (PE-18, PE-20 in *L. peruvianum*, and PE-37 in *L. hirsutum*) of the 21 genotypes. Therefore, either LDW and SDW could be used alone without great loss of accuracy in *Lycopersicon* salt-tolerance evaluation.

Although slope and EC_o provide similar salt-tolerance evaluations in this work, their meanings are rather different. EC_o is determined by Y_m , threshold, and the slope. Thus, EC_o should be an important parameter for evaluating the salinity tolerance of tomato cultivars that could be used directly by growers, because EC_o not only included the salt tolerance parameters but also Y_m . When wild species are evaluated to determine which genotypes could be used for improving salt tolerance of commercial *L. esculentum* cultivars, the slope and/or the threshold provide more information than Y_m for the evaluation of wild accessions.

Based on slope and EC_o , almost all of the most salt-tolerant accessions, PE-2, PE-45, PE-34, and PE-43, had the highest Cl_o and Na_o values. This fact suggests that the predominant salt-tolerance mechanism involves ion accumulation. Our interpretation of the data suggests that PE-2, PE-45, PE-34, and PE-43 accessions were salt-tolerant, not because they are more capable of restricting Cl^- and Na^+ uptake at high NaCl levels than other accessions, but because they have a superior ability to tolerate high levels of Cl^- and Na^+ in their tissues (Bernstein, 1963). It is also plausible that high ion accumulation is a necessary consequence of the ability to survive. Chloride and Na^+ accumulation in wild species have been reported by other researchers (Dehan and Tal, 1978; Phills et al., 1979; Tal and Shannon, 1983), suggesting that Na^+ leaf concentrations could be used as a key characteristic in evaluation of germplasm for salt-tolerance breeding programs of cultivated tomato (Rush and Epstein, 1981). However, ion concentrations in different leaves may be quite different and this may contribute to salt tolerance. Thus, the Cl^- and Na^+ accumulation in cultivated and wild tomato species was higher in mature leaves than in developing leaves (Shannon et al., 1987). However, other studies showed that the ability to regulate Na^+ , rather than Na^+ content per se, was closely correlated with salt tolerance (Sacher et al., 1983).

Cl_o values were higher than Na_o values. The Na_o : Cl_o relationship was between 0.5 and 0.6 for *L. pimpinellifolium*, *L. hirsutum*, and *L. pennellii*, but was lower for *L. peruvianum*. The different accumulation of Cl^- and Na^+ in *L. peruvianum* in relation to other wild tomato species already had been observed (Shannon et al., 1987). This differential accumulation suggests that there are differences among species in Na^+ uptake with increasing salinity. The difference may be directly related

either to the toxicities of these ions or to their roles in osmotic adjustment. Slatyer (1961) suggested that Na^+ accumulation determines reduction in development more than Cl^- .

PE-2 from *L. pimpinellifolium* seems to be a salt-tolerant accession. Since crosses between *L. pimpinellifolium* and *L. esculentum* (the tomato of commerce) are easily made and are closely related genetically (Warnock, 1988), it should, therefore, be rewarding to exploit this source of salt tolerance.

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