Theor Appl Genet (1992) 84:390–396

THEORETICAL AND APPLIED GENETICS

Breeding tomatoes for salt tolerance: inheritance of salt tolerance and related traits in interspecific populations

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Received July 30, 1991; Accepted November 11, 1991
Communicated by A. R. Hallauer

Summary. Interspecific segregating populations derived from a cross between tomato (*Lycopersicon esculentum*) cv 'M82-1-8' (M82) and the wild species *L. pennellii* accession LA-716 (Lpen716) were used to study the genetic basis of salt tolerance and its implications for breeding. BC_1 (M82 × (M82 × Lpen716)) and BC_1S_1 (progenies of selfed BC_1 plants) populations were grown under arid field conditions and irrigated with water having electrical conductivities of 1.5 (control), 10 and 20 dSm^{-1}. The evaluation of salt tolerance was based on total fruit yield (TY), total dry matter (TD) and TD under salinity relative to the control (RD). Sodium, potassium and chloride concentrations were measured in the leaves and stems. The methods for estimating heritability were adapted to BC_1 plants and BC_1S_1 families. TY, TD and RD had heritability estimates of 0.3–0.45, indicating that salt tolerance can be improved by selection. Genetic correlations between traits indicated that high yield may be combined with salt tolerance and that ion contents are not likely to provide an efficient selection criteria for salt tolerance. Genetic correlations between performances under various salinity levels suggested that similar mechanisms affect the responses to salinity treatments of 10 and 20 dSm^{-1}. Responses to "paper" selection confirmed that salt tolerance of the tomato may be improved by selection, and that this selection should be based on dry matter and yield parameters under salinity.

Key words: Salt tolerance – *Lycopersicon esculentum* – *L. pennellii* – Heritability – Genetic correlation – Selection

* Passed away May 1986

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Introduction

It is now 50 years since the genetic approach was proposed as a possible means towards the improvement of cultivation in saline ecosystems (Lyon 1941). During these years, the tomato, *Lycopersicon esculentum*, and its salt-tolerant wild relatives, *L. pennellii, L. cheesmanii* and *L. peruvianum,* have been among the most thoroughly explored species with regard to genetic aspects of salt tolerance. When it comes to the inheritance of salt tolerance, most investigations have not gone further than an evaluation of its inheritance based on the performances of parental lines and their early generation progenies, F_1 and F_2. Nevertheless, they have shown that salinity tolerance is a quantitative multigenic-controlled trait, and hence a quantitative genetic approach is required in order to establish the theoretical basis for breeding (Jones 1986).

In the design of an effective breeding strategy, it is of critical importance to acquire a better understanding of the genetic basis of salt tolerance and related traits, and of the interactions of these traits among themselves and with the environment. The ratio between the genotypic and phenotypic variability, known as heritability, indicates the potential efficiency of a selection process. Genetic correlations between traits indicate the likelihood of desirable traits becoming combined as well as the potential usefulness of indirect selection. Genetic correlations between performances at different salinity levels can provide information on the resemblance between mechanisms acting in these environments and can facilitate the choice of the salinity level at which selection should be performed.

In a previous paper we reported on the salt tolerance of field-grown tomato cultivars and wild *Lycopersicon* accessions (Saranga et al. 1991). *L. pennellii* and *L. peru-*

vianum showed higher salt tolerance levels than *L. esculentum* and *L. cheesmanii,* and even higher tolerance was shown by an interspecific F_1 (*L. esculentum* × *L. pennellii*). It was concluded that *L. pennellii,* may be utilized to improve the salt tolerance of the tomato. The tolerance of *L. pennellii, L. peruvianum* and the F_1 was found to be associated with (1) their ability to minimize salinity-induced changes in the potassium and sodium ratio and (2) accumulation of chloride in the leaves and stems (Saranga et al. 1992). We report here on the heritability of growth, yield and ion contents, on genetic correlations and on responses to selection of interspecific tomato populations grown under arid field conditions with saline water irrigation.

Materials and methods

Plant materials

Interspecific segregating populations derived from a cross between *L. esculentum* cv 'M82-1-8' (M82) and the wild salt-tolerant species *L. pennellii* accession LA-716 (Lpen716) were examined for salt tolerance. The plants were grown under arid land field conditions at the Ramat Negev Experimental Station and irrigated with water having electrical conductivities (ECi) of 1.5 (control), 10 or 20 dSm^{-1}. Each population was grown with three control lines, M82, Lpen716 and their hybrid progeny (F_1).

In 1984, 600 BC_1 (M82 × (M82 × Lpen716)) plants were examined in two main plots per treatment. In 1986, 99 families of BC_1S_1 plants (progenies of 99 self-fertilized BC_1 plants grown in 1984) were examined using a split-plot design (salinity in main plots) in six replications with a single plant per subplot (total of 1782 plants). The families included in this experiment were randomly selected from progenies of BC_1 plants grown under the ECi = 10 and 20 dSm^{-1} treatments. Because many BC_1 plants were sterile or bore only a few seeds, it may be assumed that there was unintentional selection for high fertility. In 1985, 1000 F_2 (selfed F_1 (M82 × Lpen 716)) plants were examined and used only for scaling tests (among the analyses reported hereafter).

At the end of the growing season each plant was harvested individually and the total dry matter (TD) and total fresh fruit yield weight (TY) were determined. Relative total dry matter (RD) was calculated for BC_1S_1 plants as the ratio between the TD of each salinity-treated plant and the mean TD of its family under control conditions. TD, TY and RD were used as parameters of salt tolerance of BC_1S_1 plants, whereas for BC_1 plants only TD was used because of their high rate of infertility and the inability to relate each plant to the same genotype under the control treatment. Concentrations of sodium, potassium and chloride in leaves (respectively, NaL, KL and ClL) and in stems (respectively, NaS, KS and ClS) were measured. Details of ambient conditions, management, harvesting procedure and ion determinations, as well as the results for the control lines have been reported previously (Saranga et al. 1991, 1992).

Preliminary data processing

SAS software was used for all the statistical analyses performed in this study (Ray 1982).

The following preliminary analyses were conducted.

1) Scaling tests were performed, based on BC_1, F_2 and BC_1S_1 populations (Mather and Jinks 1971). These confirmed that for salt tolerance and most related traits, excluding KL and the ratios KL/NaL and Ks/NaS, the additive – dominance model was valid.

2) The effect of parental treatment (ECi = 10 or 20 dSm^{-1}) on offspring performance was analyzed and found not significant. All BC_1S_1 plants were therefore regarded as a single population, except when calculations included parental performance.

Heritability

Data pertaining to the BC_1 plants and their progenies, BC_1S_1, were used to calculate heritability (h^2) estimates. In these populations, some expectations of variance and covariance can be determined only for the sum of two backcross populations (F_1 backcrossed with each of the parents) or their selfed progenies (Mather and Jinks 1971, p 136). Since only one backcross population and its progenies were studied, we had to assume that the two populations would have equal variance components. The expectations of variance and covariance are:

$$\sigma^2_{(BC_1)} = \tfrac{1}{2}V_A + V_D + V_E \quad (1)$$

$$\sigma^2_{b(BC_1S_1)} = \tfrac{1}{2}V_A + \tfrac{1}{4}V_D \quad (2)$$

$$\sigma^2_{w(BC_1S_1)} = \tfrac{1}{2}V_A + \tfrac{1}{2}V_D + V_E \quad (3)$$

$$Cov_{(BC_1, BC_1S_1)} = \tfrac{1}{2}V_A + \tfrac{1}{2}V_D \quad (4)$$

where σ^2, σ^2_b and σ^2_w are, respectively, the total variance, variance between families, and variance within families; Cov is the covariance; and V_A, V_D and V_E are, respectively, the additive, dominant, and environmental (non-genetic) variances.

Two methods were employed in the calculations of h^2 estimates (Cahaner and Hillel 1980).

1) Intraclass correlation (t) was calculated on the basis of BC_1S_1 families by a nested analysis of variance, and used for estimation of heritability as follows:

$$h^2_0 = 2t = \frac{2\sigma^2_b}{\sigma^2_b + \sigma^2_w} = \frac{V_A + \frac{1}{2}V_D}{V_A + \frac{3}{4}V_D + V_E} \quad (5)$$

The significance of σ^2_b was examined by the F test. The standard error of h^2 (σh^2) was calculated according to the following approximate formula (Falconer 1981, p 168):

$$\sigma h^2 = 2\sigma t = 2\sqrt{(8t/N)} \quad (6)$$

where N is the total number of individuals examined.

2) Parent – offspring correlation (R) between performances of BC_1 plants and their BC_1S_1 progenies was calculated and used for estimation of heritability as follows:

$$h^2_{po} = 1.414\,R = \frac{1.414\,Cov(p,o)}{\sqrt{(\sigma^2_p \cdot \sigma^2_o)}} = \frac{1.414\,(\frac{1}{2}V_A + \frac{1}{2}V_D)}{\sqrt{((\frac{1}{2}V_{Ap} + V_{Dp} + V_{Ep})(V_{Ao} + \frac{3}{4}V_{Do} + V_{Eo}))}} \quad (7)$$

where p and o indicate the parent and offspring populations, respectively.

The correlation coefficients between performances of individual progenies (BC_1S_1) and those of their parents (BC_1) were calculated for each combination of parental treatment (10 or 20 dSm^{-1}) and offspring treatment (1.5, 10 and 20 dSm^{-1}). Differences between the two correlation coefficients for each parental group and their progenies tested under a certain treatment were examined by the t test and found not to be significant (Steel and Torrie 1980, p 190). Correlation coefficients were also calculated for the entire population under each offspring treatment, while adjusting for the effect of parental treatment by a

nested (families within parental treatment) analysis of variance and covariance. There was only one degree of freedom for parental treatments; we therefore calculated the confidence limits of h^2 as it was based on a regular correlation (Steel and Torrie 1980, p 189).

Genetic correlations between traits

Two types of genetic correlations (r_g) were calculated.

1) Genetic correlations between the various traits of the BC_1S_1 population were calculated as follows (Cahaner and Hillel 1980):

$$r_g = \frac{\sigma_{b(x,y)}}{\sqrt{(\sigma^2_{b(x)} \cdot \sigma^2_{b(y)})}} \quad (8)$$

where $\sigma_{b(x,y)}$ is the between-family component of covariance for traits x and y, and $\sigma^2_{b(x)}$ and $\sigma^2_{b(y)}$ are the between-families components of variance for x and y, respectively. Estimates of r_g were calculated by a nested analysis of variance and covariance.

2) The genetic correlation between plant performances under various salinity treatments may be taken as genetic correlation between traits (Falconer 1981). Correlation coefficients were calculated between means of BC_1S_1 families in each treatment, and their expectation is:

$$r_g = \sigma^2_b + (1/n)\,\sigma^2_w = (7/12)\,V_A + (4/12)\,V_D + (1/6)\,V_E \quad (9)$$

where n is the number of offspring per family (n = 6).

Analysis of variance was performed to examine the interactions between salinity and family performances for confirmation of these genetic correlations.

Realized heritability and response to selection

"Paper" selection was used for the estimation of realized heritability (h^2_r), as follows (Falconer 1981, p 184):

$$h^2_r = R/S \quad (10)$$

where R is the response to selection and S is the selection differential

The response to direct selection and the correlated response to indirect selection were used for evaluation of the efficiency of various physiological traits as selection criteria.

"Paper" selection was performed on the BC_1 plants and their BC_1S_1 progenies, both grown under salinity treatments of ECi = 10 and 20 dSm^{-1}. The progeny population was therefore regarded as consisting of four subpopulations, each with a different combination of parent and progeny salinity treatments. Data were converted to standard deviation units and R, S and h^2_r were calculated separately for each subpopulation. Considerable differences between the subpopulations were found for R and h^2_r when a selection intensity of 20% was used, probably because of the small size of the selected population (ten parental plants). These differences were small when the selection intensity was 30%. Estimates of h^2_r and R for the entire population were therefore calculated as the mean of the four subpopulations under a selection intensity of 30%. The significance of the differences between performances of the selected plants and those of the entire population were examined by an *F* test.

Results

Distributions of the physiological parameters in the interspecific populations, BC_1 and BC_1S_1, (Table 1) were usually normal and overlapped the values for the parental lines and F_1 populations (Saranga et al. 1991, 1992). Means of the populations were usually intermediate between the two parental lines.

Table 1. Means and standard deviations of selected parameters measured in BC_1 and BC_1S_1 populations under control and saline conditions

Population and treatment (ECi, dSm^{-1})		Total dry matter g/plant	Leaves		Stems	
			K/Na	Cl meq/g DM	K/Na	Cl meq/g DM
BC_1						
1.5	Mean	975.2	9.89	0.74	8.61	0.55
	SD	518.2	6.95	0.19	4.39	0.15
10	Mean	794.1	4.24	0.91	3.89	0.66
	SD	458.3	2.84	0.23	2.01	0.16
20	Mean	637.7	2.88	0.96	2.20	0.74
	SD	417.0	3.33	0.29	1.43	0.20
BC_1S_1						
1.5	Mean	1012.8	7.43	0.99	6.51	0.52
	SD	713.7	5.10	0.41	3.14	0.15
10	Mean	936.3	3.07	1.34	3.89	0.62
	SD	645.4	1.30	0.72	1.41	0.19
20	Mean	764.0	2.33	1.30	2.56	0.71
	SD	519.8	1.03	0.60	0.99	0.19

Heritability

The heritability estimates calculated by intraclass correlation within BC_1S_1 families varied between 0.02 and 0.43 for the various physiological traits, with the estimates being highest for TD, RD, TY, and KL (Table 2). Lower heritability estimates (−0.01 – 0.37) were found by correlation between BC_1 and BC_1S_1, with TD and TY having the highest values. Estimates of heritability usually increased with increasing salinity, resulting in more traits whose h^2 estimates differed significantly from zero.

Realized heritability estimates varied between 0.10 and 0.22, with the highest values found for TD and TY (Table 2). Similar estimates were found in most cases in both selection direction; these were also similar to the estimates calculated by parent-offspring correlation.

Genetic correlations

Genetic correlations between traits estimated from BC_1S_1 population subjected to the 20 dSm^{-1} treatment, are presented in Table 3. ClL was omitted from the correlation matrix since its heritability estimate (from BC_1S_1) was not significant (Table 1), and hence the correlation between ClL and other traits could not be considered reliable. The genetic correlation coefficient varied from 0.0 to 0.9 (+ or −). Correlations between the traits indicating salt

Table 2. Heritability (h_o^2 and h_{po}^2) and realized heritability (h_r^2) estimates of physiological traits of interspecific tomato populations under various salinity treatments

Trait	Type of estimate[a]	Treatment (ECi, dSm^{-1})			Mean
		1.5	10	20	
TD	h_o^2	0.41 ± 0.12***[b]	0.43 ± 0.12***	0.39 ± 0.11***	0.41
	h_{po}^2	0.22 (0.14, 0.30)[c]	0.21 (0.13, 0.28)	0.23 (0.15, 0.31)	0.22
	h_r^2		0.18, 0.22[d]		0.20
RD	h_o^2		0.30 ± 0.10***	0.27 ± 0.09**	0.28
TY	h_o^2	0.27 ± 0.09***	0.42 ± 0.12***	0.28 ± 0.10***	0.32
	h_{po}^2	0.37 (0.30, 0.44)	0.19 (0.11, 0.27)	0.20 (0.12, 0.28)	0.25
	h_r^2		0.16, 0.14		0.15
NaL	h_o^2	0.15 ± 0.07*	0.19 ± 0.08**	0.13 ± 0.07*	0.16
	h_{po}^2	0.01 (−0.07, 0.10)	0.10 (0.01, 0.18)	0.12 (0.03, 0.20)	0.08
	h_r^2		0.10, 0.09		0.09
NaS	h_o^2	0.04 ± 0.04	0.02 ± 0.02	0.23 ± 0.09**	0.10
	h_{po}^2	0.01 (−0.07, 0.10)	0.01 (−0.08, 0.09)	0.07 (−0.01, 0.16)	0.03
	h_r^2		0.01, 0.05		0.03
KL	h_o^2	0.32 ± 0.10***	0.35 ± 0.11***	0.29 ± 0.10***	0.32
	h_{po}^2	0.12 (0.03, 0.20)	0.13 (0.04, 0.21)	0.16 (0.07, 0.24)	0.14
	h_r^2		0.10, 0.05		0.07
KS	h_o^2	0.05 ± 0.04	0.03 ± 0.03	0.18 ± 0.08*	0.09
	h_{po}^2	0.07 (−0.01, 0.16)	0.07 (−0.01, 0.15)	0.19 (0.10, 0.27)	0.11
	h_r^2		0.10, 0.07		0.08
KL/NaL	h_o^2	0.09 ± 0.06	0.21 ± 0.08**	0.17 ± 0.07*	0.16
	h_{po}^2	0.03 (−0.5, 0.12)	0.05 (−0.03, 0.14)	0.10 (0.02, 0.18)	0.06
	h_r^2		0.06, 0.13		0.09
KS/NaS	h_o^2	0.01 ± 0.02	0.06 ± 0.04	0.13 ± 0.07*	0.07
	h_{po}^2	0.01 (−0.07, 0.10)	0.03 (−0.06, 0.11)	0.06 (−0.03, 0.14)	0.03
	h_r^2		0.04, 0.10		0.07
ClL	h_o^2	0.05 ± 0.04	0.09 ± 0.05	0.10 ± 0.06	0.08
	h_{po}^2	0.21 (0.12, 0.29)	−0.01 (−0.10, 0.07)	0.05 (−0.04, 0.13)	0.08
	h_r^2		0.01, 0.03		0.02
ClS	h_o^2	0.22 ± 0.09**	0.26 ± 0.09***	0.22 ± 0.09**	0.23
	h_{po}^2	0.17 (0.08, 0.25)	0.18 (0.09, 0.26)	0.12 (0.04, 0.21)	0.16
	h_r^2		0.12, 0.14		0.13

TD, Total dry matter; RD, TD under salinity relative to control; TY, total fruit yield; NaL, NaS, concentration of sodium in leaves and stems, respectively; KL, KS, concentration of potassium in leaves and stems, respectively; KL/NaL, ratio of leaf potassium to leaf sodium; KS/NaS, ratio of stem potassium to stem sodium; ClL, ClS, concentration of chloride in leaves and stems, respectively

[a] h_o^2, based on intraclass correlation (ANOVA of BC_1S_1 offspring families); h_{po}^2, based on parent-offspring correlation (between BC_1 parents and BC_1S_1 offspring); h_r^2 based on "paper" selection at 30% intensity (according to BC_1 and BC_1S_1)

[b] Significance of estimates calculated by the h_o^2 method at the 0.05 (*), 0.01 (**) and 0.001 (***) levels.

[c] Confidence intervals of the estimates calculated according to the h_{po}^2 method

[d] Two h_r^2 estimates based on upward selection (left) and downward selection (right); each is the mean of four salinity-treated subpopulations

tolerance (TD, RD and TY) and other traits may be used to evaluate the potential of the latter to serve as criteria for indirect selection; these coefficients varied between −0.61 to 0.36. Also of interest is the correlation between the 3 traits indicating salt tolerance, from which one can draw conclusions about the feasibility of combining them in one cultivar. The correlation between RD and TD was zero ($r = -0.03$), but each of these 2 traits was positively correlated with TY. Similar results were obtained for the ECi = 10 dSm^{-1} treatment (not presented).

Table 3. Genetic correlations between physiological traits of the BC_1S_1 population under the ECi = 20 dSm^{-1} salinity treatment ($n = 490$)

Trait[a]	RD	TY	NaL	NaS	KL	KS	KL/NaL	KS/NaS	ClS
TD	−0.03	0.11	0.26	0.12	−0.13	0.26	−0.15	0.08	0.36
RD		0.50	−0.35	−0.30	−0.31	−0.30	−0.05	0.03	−0.14
TY			0.21	−0.38	−0.24	−0.61	−0.17	−0.04	−0.55
NaL				0.93	−0.04	0.24	−0.62	−0.74	0.45
NaS					−0.11	0.29	−0.65	−0.90	0.35
KL						0.42	0.77	0.32	0.00
KS							0.24	0.27	0.86
KL/NaL								0.72	−0.14
KS/NaS									0.10

[a] See footnote to Table 2 for abbreviations

Table 4. Genetic correlations between expressions of the same trait under different salinity levels in BC_1S_1 plants. Means of each family under each treatment were correlated ($n = 99$). The numbers in brackets indicate confidence intervals of the correlation coefficients

Trait[a]	Correlation coefficients		
	1.5 dSm^{-1}, 10 dSm^{-1}	1.5 dSm^{-1}, 20 dSm^{-1}	10 dSm^{-1}, 20 dSm^{-1}
TD	0.63 (0.49, 0.74)	0.56 (0.41, 0.68)	0.50 (0.34, 0.64)
RD			0.39 (0.20, 0.54)
TY	0.42 (0.24, 0.57)	0.41 (0.23, 0.56)	0.65 (0.52, 0.75)
NaL	0.33 (0.14, 0.49)	0.41 (0.23, 0.56)	0.36 (0.18, 0.53)
NaS	0.15 (−0.04, 0.34)	0.25 (0.05, 0.42)	0.24 (0.05, 0.42)
KL	0.50 (0.33, 0.63)	0.56 (0.40, 0.68)	0.57 (0.42, 0.69)
KS	0.34 (0.16, 0.51)	0.22 (0.02, 0.40)	0.29 (0.09, 0.46)
KL/NaL	0.30 (0.11, 0.47)	0.26 (0.07, 0.44)	0.46 (0.28, 0.60)
KS/NaS	0.19 (−0.01, 0.37)	0.20 (0.00, 0.38)	0.32 (0.14, 0.49)
ClL	0.09 (−0.11, 0.28)	0.02 (−0.17, 0.22)	−0.05 (−0.15, 0.24)
ClS	0.37 (0.19, 0.53)	0.45 (0.28, 0.60)	0.59 (0.45, 0.71)

[a] See footnote Table 2 for abbreviations

Genetic correlations between plant performances under the different salinity treatments were in most instances between 0.2 and 0.6, and differed significantly from zero (Table 4). The lowest correlation coefficients under all treatment combinations were found for ClL. Correlations between values for TY, KL/NaL, KS/NaS and ClS under the two salinity treatments were higher than the correlations between the control (1.5 dSm^{-1}) and each of the salinity treatments. Interactions between salinity and family were usually not significant, confirming the existence of significant genetic correlations between treatments.

Response to selection

Standardized direct and correlated responses of the salt-tolerance criteria to selection are presented in Table 5. The highest responses were found for direct selection of TD in both directions and for direct upward selection of

Table 5. Direct and correlated responses (in standard deviation units) to 30% upward and downward "paper" selection of traits indicating salt tolerance; values are means of four groups differing in salinity treatments applied to parents (BC_1) and offspring (BC_1S_1)

Trait[a]	Direct response		Indirect response					
	upward	downward	upward			downward		
			TD	RD	TY	TD	RD	TY
TD	0.22***	−0.22***		−0.09	−0.04		−0.02	0.02
TY	0.21***	−0.15*	0.04	0.03		−0.09	−0.12*	
NaL	0.11	−0.07	0.07	0.01	0.03	−0.07	0.03	−0.03
NaS	0.01	−0.05	−0.04	−0.10	0.19**	0.00	0.05	−0.11
KL	0.12	−0.05	0.09	0.03	−0.08	−0.17**	−0.19***	−0.03
KS	0.11	−0.07	0.10	0.02	0.07	−0.15*	−0.20***	−0.10
KL/NaL	0.06	−0.09	−0.03	0.00	0.02	−0.04	−0.08	0.05
KS/NaS	0.05	−0.10	−0.02	0.13*	−0.06	−0.03	−0.13*	0.16*
ClL	0.01	−0.03	−0.05	0.14*	0.20**	0.16**	−0.00	−0.04
ClS	0.13	−0.14	−0.08	−0.12	−0.05	0.06	0.07	0.07

*, ** and *** indicate a significant difference between the selected fraction and the whole population acording to the F test at the 0.05, 0.01 and 0.001 levels

[a] see footnote to Table 2 for abbreviations

TY. Significant correlated responses, either positive or negative, were also found when selection was performed according to some of the ion contents or ratios.

Discussion

Heritability of salt tolerance and related traits

Two methods were employed to estimate the heritability of salt tolerance and related traits. The estimates obtained by both methods do not reflect "narrow sense" heritability because they included, in addition to the additive variation (V_A), a part of the dominance variation (V_D). In most instances, the intraclass correlation method had higher heritability estimates than did the parent-offspring correlation method (Table 2). With the intraclass correlation method, 0.67 ($\frac{1}{2}:\frac{3}{4}$) of V_D of BC_1S_1 was added to V_A, while with the parent-offspring correlation 0.58 ($\frac{1}{2}:\sqrt{\frac{3}{4}}$) of the average V_D of BC_1 and BC_1S_1 was added (see formulas 6 and 9). This does not, however, seem to be the cause of the large differences found between the estimates. Heritability estimates calculated from intraclass correlations were based only on the BC_1S_1 population, whereas in the other method the estimates were based also on BC_1. Differences between the two populations with regard to interaction among genes and between genotypes and environments may have resulted in the observed differences between heritability estimates. Another possible explanation is that the two populations were examined separately and thus possibly differed in their V_E components.

Heritability estimates of some traits increased with increasing salinity level (Table 2). This may be a result of a greater genetic variation due to expression of genes associated with salinity tolerance and/or a smaller environmental variation.

Realized heritability estimates calculated by upward and downward selection were in most cases similar and resembled the heritability estimates calculated by the parent-offspring correlation (Table 2), probably because both estimates were based on the association between BC_1 plants and their progenies. These similarities indicate that V_A and V_E are symmetrically distributed, and therefore an estimate based on the entire population will provide a reliable prediction of a selection in any direction and of any intensity.

The highest heritability estimates found by all three methods were for the salt-tolerance criteria (TD, RD and TY). These estimates, although not very high, indicate that salt tolerance may be transferred from *L. pennellii* to *L. esculentum* and that it is heritable to the extent that it can be utilized for breeding.

Little information is available regarding the heritability of salt tolerance and related traits in tomato and other crops. A wide range of heritability estimates, 0.19–0.96, has been found for various species (Moeljopawiro and Ikehashi 1981; Jones 1984; Norlyn 1984; Ashraf et al. 1986, 1987). None of these, however, was based on species or populations like those used in our study, and comparisons are, therefore, not possible.

Genetic correlations between traits

Genetic correlations between the salt-tolerance parameters and ion contents may serve as a basis for the performance of indirect selection, which in certain circumstances may have an advantage over direct selection. Correlation coefficients between the TD, RD and TY and the ion concentrations and ratios reached a maximal value of 0.6 (Table 3). To achieve higer responses by indirect rather than by direct selection, given genetic correlations of this magnitude, the ratio between the heritabilities of the tolerance criteria and ion contents should be higher than 3 (Turner and Young 1969, p 131). Such a ratio was not obtained in our study, indicating that indirect selection based on ion contents is not capable of improving the selection process.

Questions have been raised about whether stress tolerance can be combined with high yields (Finlay and Wilkinson 1963; Rosielle and Hamblin 1981). The positive genetic correlation ($r=0.50$) found between RD and TY indicates that it is possible to combine salinity tolerance with high yields in tomato plants.

Genetic correlations between concentrations of a certain ion in leaves and stems reflect the mechanisms controlling its absorption and translocation in the plant. The high correlation (0.93) between NaL and NaS suggests that the same physiological mechanism controls sodium content in leaves and stems, whereas the lower correlation (0.42) between KL and KS suggests that the potassium concentrations in these two plant organs is at least partially controlled by separate mechanisms.

Genetic correlations between performances under various treatments

The positive genetic correlation between the same parameter under various treatments (Table 4) indicates that there is no interaction between these growth conditions; this was confirmed by the analysis of variance. For ClL, however, the correlation coefficients – like the heritability estimates – were nearly zero; both results indicate a small genetic variation and/or large environmental variation in the expression of ClL.

The correlation coefficients between the two salinity treatments were a little higher than those between each treatment and the control (Table 4). The traits measured here are probably affected by certain genes under any environmental conditions; this would explain the correlation between control and salinity treatments. The higher correlation between the two salinity treatments may be

due to additional genes that are expressed only under salinity. To select for these salinity-induced genes, selection for salt tolerance should be performed under saline conditions. The genetic correlation between the two salinity treatments also indicates that selection under one salinity treatment may also reveal a higher tolerance under the other treatment.

Selection criteria

The highest response to direct selection was exhibited by TD and TY, in line with the high heritability estimates for these traits (Table 5). This supports our conclusion, based on the heritability estimates, that it seems possible to improve growth and yield under salinity by selection.

In most instances where a significant response to indirect selection was found, it was in agreement with our results regarding the effects of ion contents on growth (Saranga et al. 1992). Those results were, however, contradicted by the positive response of RD to upward selection according to ClL and the positive responses of TY to upward selection according to NaS and ClL and also to downward selection according to KS/NaS. The heritability estimates of the 3 traits involved, NaS, KS/NaS and ClL, were nearly zero, and the estimates of indirect response to selection according to these traits are therefore unreliable.

As expected, the responses of the salt-tolerance criteria (TD, RD and TY) to indirect selection were lower than their responses to direct selection (Table 5). Hence, indirect selection should be used only if it has some practical or economic advantage. Measurement of TD and TY is less time-consuming and labor-intensive than measurement of ion contents, and thus there is no advantage to be gained from using indirect selection for these traits. The situation is different when selecting for RD. Evaluation of RD is not possible in early generations, such as BC_1 and F_2, and in advanced generations it may be estimated on the basis of family averages with a certain level of inaccuracy. Indirect selection for RD, while using ion contents (KS/NaS for example) as a criterion, may therefore be useful.

The results presented in this study demonstrate that it is possible to improve the salt tolerance of tomato. This conclusion has lead to the development of 120 different *L. esculentum* lines containing small chromosome segments of *L. pennellii* covering 95% of the genome, as defined by RFLP analysis (Eshed et al. 1992). These lines are being studied under salinity stress in order to map genes contributing to salt tolerance in the tomato.

Acknowledgements. This research was conducted within the framework of the Cooperative Arid Land Agricultural Research-Egypt-USA-Israel (CALAR), funded by the US Agency for International Development (Contract No. NEB-0170-A-00-2047-00) and administered by the San Diego State University Foundation.

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