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Salt tolerance in *Lycopersicon* species. II. Genetic effects and a search for associated traits

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Abstract. Eleven quantitative traits, mostly related to tomato plant growth and fruit set, and their association with salt tolerance in terms of fruit yield under a 171.1 mM NaCl treatment have been investigated in 206 progeny derived from an interspecific hybrid, *L. esculentum* × *L. pimpinellifolium*, by self-pollination. None of the traits were highly correlated phenotypically to salt tolerance; however, the immunologically-detected presence of peptide 2′ was significantly associated with high total fruit weight (TW) and number (FN) under saline treatment. Broad-sense heritability was estimated for these two salt-tolerance components as 53.44 and 72.59 %, respectively. Non-additive gene effects, which have to be considered in a breeding program for salt tolerance, have been detected in TW, FN and in average fruit weight (FW). Given that different types of gene action have been found depending on the presence or absence of a high NaCl concentration in the nutrient solution, a different set of genes, or genes, differently regulated, must be involved in the expression of TW, FN and other fruit-related characters depending on this environmental condition.

Key words: Salt tolerance – *Lycopersicon* – Heritability – Genetic correlations

Introduction

Breeding for salt tolerance in higher plants is widely recognized as an important aspect of improving crop productivity in salt-affected areas (Epstein et al. 1980). In a companion paper (Asins et al. 1993), the character of salt tolerance under different saline levels was analyzed in 11 lines belonging to five *Lycopersicon* species. As a consequence, we decided to use salt-tolerant lines of *L. pimpinellifolium* as donors of salt tolerance (at a conductivity of 15 dS/m) in tomato breeding programs.

Screening large numbers of genotypes on naturally saline soils for improved salinity tolerance is not feasible because of the extreme variability in soil salinity both spatially and temporally (Hajrasuliha et al. 1980; Richards 1983). To avoid this variability in screening programs, plants are often grown in nutrient solutions to which NaCl has been added. Selection is then the next problem. It is frequently based on the ability to germinate or survive, often under extreme NaCl concentrations (Epstein et al. 1980; McGuire and Dvorak 1981). Unfortunately, germination and survival in salinized nutrient solutions may bear no relationship to growth and yield of plants in saline soils (Rawson et al. 1988). In fact, the salt tolerance of young tomato plants is not well correlated with that of mature plants (Shannon 1979; Guerrier 1984; Norlyn and Epstein 1984). Other characters, such as ion content, have not been found to provide an efficient selection criterion for salt tolerance (Saranga et al. 1992). Therefore, to identify characters, easily measured at early developmental stages, that correlate with salt tolerance in terms of yield, would be very useful for salt tolerance breeding programs. Furthermore, given that a wild species, although most closely related to the cultivated one (Bretó et al. 1992), has been used as the donor of salt tolerance, recovery of the cultivated genome becomes an important but difficult component of the breeding program. Marker-assisted selection would be most valuable for this purpose (Landry and Michelmore 1987; Nienhuis and Helentjaris 1989; Young and Tanksley 1989; Walton 1990).

A better understanding of the genetic basis of salt tolerance is crucial in order to design an effective breeding strategy. Very recently, Saranga et al. (1992) found heritability estimates of 0.30–0.45, indicating that salt tolerance of the tomato can be improved by selection. However, nothing is yet known about the types of gene action involved in the salt tolerance of a mature tomato plant.

Consequently, the objectives of the present paper are to study:

(1) several characters, mostly related to plant growth and fruit

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set, that could correlate with salt tolerance in terms of yield in an F_2 population derived from the interspecific hybrid *L. esculentum* × pimpinellifolium.
(2) the existence of an association between the presence of the previously reported peptides 2 or 2′ (Asins et al. 1993) and the salt-tolerance phenomenon before continuing a study of these peptides at the molecular level.
(3) the types of gene effects involved in the expression of both yield and vegetative characters under control and two saline levels (15 and 22 dS/m).

Materials and methods

The material studied included two parental lines differing in NaCl tolerance, *L. esculentum* cv Madrigal and *L. pimpinellifolium* line 1 (Asins et al. 1993), their interspecific hybrid (F_1), its reciprocal (F_1'), and 206 progeny derived from the hybrid by self-pollination (F_2). Nine plants per uniform genotype and treatment were grown on sand and irrigated with nutrient solution. Except for the F_2 population, all genotypes were kept under treatment A with one-half Hoagland solution (conductivity of 1 dS/m) as a control. Parental lines and F_1 and F_2 were all grown under treatment B involving a control solution plus 171.1 mM of NaCl (conductivity of 15 dS/m). Parental lines, the hybrid and the reciprocal were also grown under treatment C employing a control solution plus 256.65 mM of NaCl (conductivity of 22 dS/m). Plants were cultured in a greenhouse with both photoperiod (12 h light) and temperature (25 °C ± 10 °C) control, from January to July 1991. The final conductivity of the treatment was determined as described by Asins et al. (1993).

Three yield components, five yield-related characters, five vegetative characters and a biochemical character were studied by a two-way ANOVA (saline treatment by genotype) and correlation analysis: "fruit number" (FN), "total fruit weight" in grams (TW), "average fruit weight" in grams (FW), "fruit set" as the percentage of flowers from the second (FS2) and third raceme (FS3) that yielded fruits, "number of flowers" at the second (FL2) and third raceme (FL3) and the average of both (FL23), "earliness" (EAR) as the number of weeks elapsed since treatment B or C began and until the first mature tomato was produced by the plant, "height" (HEI) of the plant in cm at the sixth week of

Table 1. Means and standard deviations, and non-additivity (NA) and epistatic (EP) effect contrasts for Madrigal, line 1, F_1, and F_2. "T" means treatment, NS is Non significant, * and ** mean significant at $P < 0.05$ or 0.01 respectively. See text for trait abbreviations

Trait	T	Madrigal	Line 1	F_1	F_2	NA	EP
FL2	A	5.10 ± 1.20	13.50 ± 6.60	11.44 ± 0.88		NS	
	B	4.50 ± 1.19	6.67 ± 2.55	9.40 ± 1.58	6.96 ± 3.49	**	NS
	C	2.67 ± 2.08	13.00 ± 5.29	8.50 ± 2.81		NS	
FL3	A	4.60 ± 2.22	17.70 ± 8.23	10.89 ± 1.76		NS	
	B	3.25 ± 1.67	7.11 ± 3.41	9.00 ± 1.33	7.59 ± 5.87	**	NS
	C	0.00 ± 0.00	12.75 ± 3.30	8.00 ± 1.67		NS	
FL23	A	4.85 ± 1.43	15.60 ± 7.14	11.17 ± 1.12		NS	
	B	3.87 ± 0.99	6.89 ± 2.85	9.20 ± 1.42	7.13 ± 3.94	**	NS
	C	1.33 ± 1.04	12.87 ± 3.50	8.25 ± 1.60		NS	
FS2	A	0.57 ± 0.26	0.79 ± 0.39	0.90 ± 0.19		*	
	B	0.20 ± 0.30	0.64 ± 0.30	0.65 ± 0.32	0.44 ± 0.37	NS	NS
	C	0.00 ± 0.00	0.50 ± 0.39	0.78 ± 0.42		*	
FS3	A	0.21 ± 0.29	0.85 ± 0.31	0.91 ± 0.23		**	
	B	0.00 ± 0.00	0.61 ± 0.13	0.63 ± 0.40	0.54 ± 0.36	*	NS
EAR	A	6.50 ± 0.55	5.00 ± 0.00	3.33 ± 1.03		**	
	B	6.00 ± 1.09	6.33 ± 1.03	1.33 ± 0.52	6.88 ± 4.00	**	**
	C	8.00 ± 0.00	5.60 ± 1.95	3.17 ± 0.41		**	
TW	A	272.66 ± 80.6	70.03 ± 30.7	137.03 ± 35.5		NS	
	B	26.63 ± 11.6	12.02 ± 2.51	49.35 ± 22.7	30.09 ± 25.1	**	NS
	C	14.94 ± 4.45	6.46 ± 7.21	33.56 ± 12.1		**	
FN	A	5.15 ± 2.14	89.67 ± 38.3	31.83 ± 8.93		**	
	B	1.33 ± 0.51	22.00 ± 4.10	16.33 ± 7.06	13.40 ± 10.3	NS	NS
	C	1.00 ± 0.00	13.20 ± 12.9	9.17 ± 4.26		NS	
FW	A	56.63 ± 13.9	1.15 ± 0.25	7.20 ± 0.65		**	
	B	21.78 ± 11.2	0.75 ± 0.10	3.78 ± 0.72	2.82 ± 1.81	**	**
	C	14.94 ± 4.45	0.49 ± 0.19	4.11 ± 0.79		**	
SS	A	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00		NS	
	B	3.00 ± 0.00	2.00 ± 0.00	3.17 ± 0.41	2.63 ± 0.98	**	NS
	C	3.33 ± 0.52	3.83 ± 1.17	3.33 ± 0.52		NS	
LS	A	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.0		NS	
	B	61.00 ± 41.3	83.33 ± 33.3	46.80 ± 37.7	53.06 ± 37.3	NS	NS
	C	21.33 ± 3.26	20.83 ± 8.49	20.50 ± 3.94		NS	
ID	A	6.15 ± 0.67	3.85 ± 0.75	7.40 ± 1.68		**	
	B	4.40 ± 1.29	2.61 ± 0.65	4.75 ± 1.13	4.06 ± 1.82	*	NS
	C	3.25 ± 2.07	3.33 ± 0.76	6.50 ± 1.47		**	
HEI	A	107.40 ± 20.7	99.40 ± 29.3	120.00 ± 0.00		**	
	B	47.95 ± 7.66	57.06 ± 15.5	75.44 ± 10.3	54.14 ± 20.9	**	*
	C	34.08 ± 8.17	55.12 ± 24.3	64.00 ± 6.23		*	
PC	B	3.70 ± 1.18	2.39 ± 0.86	3.38 ± 0.48	4.50 ± 1.62	NS	**

treatment (plants higher than 120 cm were recorded as 120 cm), "internodal distance" (ID) in cm between the 9th and the 10th leaf, "stress symptoms" (SS) at the 6th week of treatment classified in five classes according to the chlorosis of the leaves and the apical meristem and the degree of defoliation, etc. (the worse looking the plant, the higher the index), "life span" (LS) as the number of weeks until the plant died (an arbitrary value of 100 was given to those plants that lasted the whole experiment), and the "protein concentration" (PC) of leaf extracts (at the 6th week after treatment) quantified by means of the Bio-Rad Protein assay as equivalents of μg of BSA.

For all the above traits, non-additive and epistatic gene action were estimated by the following contrasts (Wricke and Weber 1986, pg 67):

$2F_1 - (P_1 + P_2)$ for non-additivity
$4F_2 - 2F_1 - (P_1 + P_2)$ for epistasis

where P_1 and P_2 stand for both parental lines. The significance of the contrast was established by a t-test. Given that for many variables the variances were very different according to the genotypes (parentals, F_1 and F_2), tests were based on the specific variances not on a pooled estimate.

To estimate the broad-sense heritability, the non-genetic variance (V_e) was obtained as a weighted average (1:1:2) of the variances of the parentals and the F_1 for the reason given above. Since variance among F_2 progeny (V_p) is the sum of both genetic (V_g) and non-genetic variances, heritability was calculated as the ratio V_g/V_p.

Leaf protein extractions and polyacrylamide-gel electrophoresis were performed as described in Conejero and Semancik (1977). Western blots containing samples from all plant material, grown under conditions A and B, at the 6th week after treatment B began, were incubated with polyclonal antibody 2 following the procedure described in Asins et al. (1993). To study the association between the fruit yield characters and peptides 2 or 2′ and the presence of TMV virus, a one-way ANOVA was performed using presence/absence as the classification level.

Results

Means and standard deviations, and non-additivity and epistatic contrasts for all quantitative characters are summarized in Table 1. Five of them show the same type of gene action independent of the treatment: LS is a completely additive trait and EAR, FW, ID and HEI show a non-additive behaviour. Epistatic effects were detected in EAR, FW, HEI and PC. For the others, the occurrence of dominance effects depend on the treatment. Therefore, a different set of genes, or genes functioning differently, are involved in the expression of these characters depending on the treatment. Phenotypic variances are clearly related to the magnitude of the means; the higher the mean, the higher the variance.

Regarding the behaviour of the reciprocal in comparison with the hybrid, significant differences were found between them in ID, EAR, HEI and LS (Fig. 1).

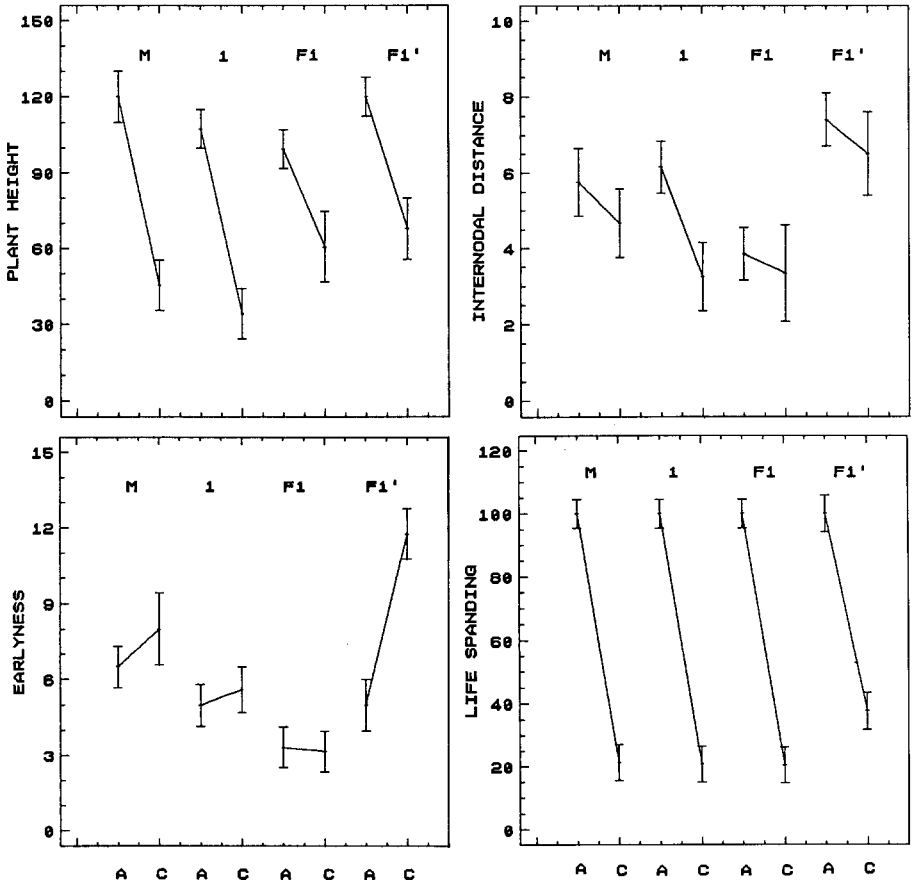

Fig. 1. Genotype-treatment interactions for plant height, internodal distance, earliness and life span. See text for meaning of treatments A and C. *M*, 1, F_1 and F_1' stand for Madrigal, line 1, the interspecific hybrid and its reciprocal, respectively

Table 2. Coefficients of correlation among all the characters and broad-sense heritability (h^2) of characters for the F_2 under salinity treatment B. "–" means estimated V_e greater than V_p at F_2. See text for character abbreviations

Trait	TW	FN	FW	h^2
FL2	0.45	0.37	0.27	73.56
FL3	0.52	0.44	0.26	86.97
FL23	0.32	0.34	0.18	78.86
FS2	0.40	0.30	0.17	41.67
FS3	0.46	0.36	0.13	38.46
EAR	−0.31	−0.12	−0.27	95.00
TW	1.00	0.68	0.58	53.44
FN	0.68	1.00	0.13	72.59
FW	0.58	0.13	1.00	–
SS	−0.42	−0.27	−0.40	91.67
LS	0.39	0.49	0.33	–
ID	0.32	0.19	0.22	64.95
HEI	0.45	0.39	0.22	84.28
PC	0.40	0.21	0.30	75.19

Table 3. Mean values for the fruit yield characters and protein concentration in the F_2 under treatment B, and association to the presence of peptides 2 and 2′, and TMV. "+", "−" and NS mean presence, absence and non-significant, respectively

Trait	2′ −/+	2 −/+	TMV −/+	2′-TMV −/+
TW	27/47	NS	NS	28/50
FW	NS	3.0/1.9	2.7/4.3	NS
FN	12/20	NS	NS	12/21
PC	4.1/6.4	NS	NS	4.1/6.3

In order to determine whether or not any of these characters were related to salt tolerance in terms of yield, phenotypic correlations among FN, TW and FW, and the whole set of characters were calculated in the F_2 population (Table 2). No important correlation seems to exist. The characters that showed the highest coefficients were, FL3, LS and SS regarding TW, FN and FW, respectively.

Broad-sense heritability was calculated for all characters in the F_2 population under treatment B (Table 2). There are two characters, FW and LS, where, due to the large variability found in Madrigal, accompanied, in the case of FW, by a large mean, the estimated non-heritable component of variability is greater than the estimated total variance. Broad-sense heritability of salt tolerance, expressed as TW and FN under salinity, was estimated as 53.44 and 72.59%, respectively.

Under treatment B at the time of the analysis peptide 2′ was present only in line 1. The χ^2 value for its segregation ratio in the F_2 under a 1:3 presence vs absence hypothesis, was 4.66 (significant at 5%). Other hypotheses such as 1:15 or 7:9, resulted in greater χ^2 values.

Table 3 contains the results from the one-way analysis of variance for the yield characters and the concentration of protein in the leaf extracts according to the immunologically detected presence/absence of peptides 2 and 2′, and of TMV virus coat protein, for the F_2 plants. The presence of TMV was detected from the leaf proteinograms (see Fig. 2 in Asins et al. 1993) in 12 plants of the F_2. The presence of peptide 2′ proved to be associated with salt tolerance. The presence of peptide 2 was associated with a decrease in FW and the presence of TMV was, unexpectedly, associated with an increase in this same yield character. Although the presence of TMV could be a confounding factor in the experiment, it does not seem so, given that, as is shown in Table 3 (under the 2′-TMV heading), if data from plants with TMV are omitted from the analysis, the presence of 2′ peptide is still associated with salt tolerance, and even increases the difference between the means of the two classes. The concentration of proteins did not relate to any of the yield characters, but did relate to the presence of peptide 2′.

Discussion

In evaluating the data from Table 1, two crucial trends for the breeding program become apparent. For the three fruit-yield components: total weight (TW), fruit number (FN) and average fruit weight (FW), non-additive gene effects have been detected and, except for FW, different types of gene action have been found depending upon the presence of NaCl in the nutrient solution. Saranga et al. (1992) found that genetic correlations between performance under 10 and 20 dS/m treatments were higher than those between each treatment and the control, suggesting the existence of additional genes that would be expressed only under conditions of salinity. This, of cource, is not the only way to explain their and our results. Some genes involved in the expression of these characters could be regulated (or interact) differently depending on the amount of NaCl in the nutrient medium. Not only do TW and FN show different types of gene action depending on the treatment but other features related to fruit yield, such as "number of flowers" and "fruit set" are also affected. As mentioned in the companion paper, under 15 dS/m, the fruit set by the Edkawi cultivar never fills. The other cultivar, Madrigal, also survives and flowers under this treatment but the flowers fall off after opening; moreover, there are F_2 genotypes with a maximum "life span" (LS) that do not flower at all. Flowering, fruit set and fruit development are important, highly regulated, plant processes to which not very much attention has been paid in saline environments, although lately (XIIIth EUCARPIA Congress 1992) increasing interest has been focused on the relationship between reproductive biology and plant breeding.

Except for the "number of flowers at the third raceme", none of the coefficients of correlation for the characters involved in the present study with the yield components resulted in F_2 values higher than 0.50 (Table 2). As expected, it is one of the characters related to the reproductive process (FL3) whose coefficient of correlation with yield (TW) under salinity reaches the highest value. Although we would not recommend the use of this character for salt-tolerance screening, it again points to the importance of flowering, fertility and fruit development in understanding the phenomenon of salt tolerance in terms of fruit yield.

The four characters related to plant vigour, earliness, life span, internodal distance and plant height, all show maternal effects in their inheritance. Similarly, Fooland and Jones (1991) found significant maternal effects in the germination performance under salt stress, suggesting the use of the salt-tolerant genotype and progeny as the maternal parent in a breeding program to improve salt tolerance at the germination stage.

The estimated broad-sense heritability must be considered as an upper limit of the heritable component of total variability. Therefore, given that we have detected dominance effects, its estimated value for TW (53.44%) is in agreement with the *sensu-strictu* heritability of 30–45% obtained in backcrosses (Saranga et al. 1992). Salt tolerance, considered in terms of total fruit yield, is a quantitative character where the environmental or non-heritable component of variation is almost as important as the genetic one. Additionally, using *L. pimpinellifolium* as the salt-tolerant donor has resulted in a large genetic variance in FN under conditions of salinity, with 72.59% of the total variance in the F_2.

Our results agree with those reported by Saranga et al. (1992), suggesting that for salt-tolerance breeding programs, beyond 10 dS/m, selection or screenings should be performed under saline conditions. This contrasts with the results obtained in low and moderate (less than 7 dS/m) saline treatments by Kelman and Qualset (1991) in wheat. Here selection in low salinity environments would be expected to produce cultivars with a high yielding potential for environments with moderate salinity stress (around 7 dS/m). Furthermore, the additive, dominance and epistatic effects in the main fruit yield components of salt tolerance, should permit the development of recombinant inbred lines from the F_2, containing the salt tolerance quantitative trait loci (QTL) of line 1 and recovering most of the genome of *L. esculentum*. This, coupled with recurrent selection for specific combining ability of the lines with a good tomato cultivar, seems to be the most adequate strategy for breeding salt-tolerant (above 10 dS/m) tomatoes.

One quantitative character, peptide 2′, has been found statistically associated with salt tolerance at two of its yield components, TW and FN. The use of a polyclonal antibody to detect the presence of 2′ makes it very difficult to distinguish between heterozygotes and homozygotes for its absence. This explains the expectation of a presence vs absence segregation ratio of 1:3. The significant deviation found regarding this hypothesis is probably explained by the interspecific origin of the F_2. Rick (1969, 1972) reported significant deviation from Mendelian expectations in segregations of the interspecific cross *L. esculentum* × *L. pennellii*. Tanksley (1986) also observed abnormal gene flow in isozyme marker segregations in two tomato interspecific crosses as well as in one interspecific cross in pepper.

Surprisingly, the presence of TMV is statistically associated with an increase of FW. The huge amount of TMV coat protein detected in the infected plants suggests that this protein could be acting as an osmolyte, allowing the fruit to grow in spite of the high external osmotic pressure. If it was possible to genetically modify a plant to overexpress an innocuous peptide in the fruit as a response to high salt stress this could be considered as a target for producing salt-tolerant crops whose fruits are the economically important part.

In conclusion, salt tolerance, defined as total fruit weight in our F_2 tomato population grown under 15 dS/m, is a quantitative trait where the non-heritable component of variation is almost as important as the genetic one. The genetic component involves not only additive but also non-additive effects which need to be considered in the design of a breeding program for salt-tolerant plants and in the statistical model used to locate the salt tolerance QTL (Carbonell et al. 1992). The NaCl concentrations used in the nutrient solutions affect the type of gene effects found for most fruit set characters, suggesting differences in gene regulation. To our knowledge, this is the first time a peptide or protein has been found associated with salt tolerance in terms of fruit yield. This statistical association needs further research at the molecular level to elucidate its possible functional meaning and to provide a DNA probe that could be used as a salt-tolerance marker at seedling stage.

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References

Asins MJ, Bretó MP, Cambra M, Carbonell EA (1993) Salt tolerance in *Lycopersicon* species. I. Character definition and changes in gene expression. Theor Appl Genet 86:737–743

Bretó MP, Asins MJ, Carbonell EA (1992) Distribution of genetic variability in *Lycopersicon* species and their genetic relationships. Theor Appl Genet 86:113–120

Carbonell EA, Gerig TM, Balansard E, Asins MJ (1992) Interval mapping in the analysis of non-additive quantitative trait loci. Biometrics 48:305–315

Conejero V, Semancik JS (1977) Analysis of the proteins in crude plant extracts by polyacrylamide slab-gel electrophoresis. Phytopathology 67:1424–1426

Epstein E, Norlyn JD, Rush DW, Kingsbury RW, Kelley DB, Cunningham GA, Wrona AF (1980) Saline culture of crops: a genetic approach. Science 210:399

Fooland MR, Jones RA (1991) Genetic analysis of salt tolerance during germination in *Lycopersicon*. Theor Appl Genet 81:321–326

Guerrier G (1984) Selectivité de fixation du sodium an niveau des embryons et des jeunes plants sensible or tolerants au NaCl. Can J Bot 62:1791–1792

Hajrasuha SN, Baniabbassi J, Metthey J, Nielson DR (1980) Spatial variability in soil sampling for salinity studies in southwest Iran. Irrig Sci 1:197–208

Kelman WM, Qualset CO (1991) Breeding for salinity-stressed environments: recombinant inbred wheat lines under saline irrigation. Crop Sci 31:1436–1442

Landry BS, Michelmore RW (1987) Methods and applications of restriction fragment length polymorphism analysis to plants. In: Bruening G, Harada J, Kosuge T, Holleander A (eds) Tailoring genes for crop improvement. Plenum press, New York, pp 25–44

McGuire PE, Dvorak J (1981) High salt tolerance in wheat grasses. Crop Sci 21:702–705

Nienhuis J, Helentjaris T (1989) Simultaneous selection for multiple polygenic traits through RFLP analysis. In: Helentjaris T, Burr B (eds) Development and application of molecular markers to problems in plant genetics. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York, pp 107–112

Norlyn JD, Epstein E (1984) Variability in salt tolerance of four triticale lines at germination and emergence. Crop Sci 24:1090–1092

Rawson HM, Richards RA, Munns R (1988) An examination of selection criteria for salt tolerance in wheat, barley and *Triticale* genotypes. Aust J Agri Res 39:759–772

Richards RA (1983) Should selection for yield in saline conditions be made on saline or non-saline soils. Euphytica 32:413–438

Rick CM (1969) Controlled introgression of chromosomes of *Solanum pennellii* into *Lycopersicon esculentum*: segregation and recombination. Genetics 62:753–768

Rick CM (1972) Further studies on segregation and recombination in backcross derivatives of tomato species hybrid. Biol Zbl 91:209–220

Saranga Y, Cahaner A, Zamir D, Marani A, Rudich J (1992) Breeding tomatoes for salt tolerance: inheritance of salt tolerance and related traits in interspecific population. Theor Appl Genet 84:390–396

Shannon MC (1979) In quest of rapid screening techniques for plant salt tolerance. Hort Science 14:587–589

Tanksley SA (1986) Introgression of genes from wild species. In: Tanksley SD, Orton TJ (eds) Isozymes in plant genetics and breeding. Elsevier, Amsterdam, pp 331–337

Walton M (1990) Application of RFLP technology to applied plant breeding. In: Bennett AB, O'Neil SD (eds) Horticultural biotechnology. Wiley-Liss, New York, pp 335–346

Wricke G, Weber WF (1986) Quantitative genetics and selection in plant breeding. de Gruyer, New York

Young ND, Tanksley SD (1989) Graphics-based whole-genome selection using RFLPs. In: Helentjaris T, Burr B (eds) Development and applicaton of molecular markers to problems in plant genetics. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York, pp 123–129