Theor Appl Genet (1993) 86:737–743

THEORETICAL AND APPLIED GENETICS

Salt tolerance in Lycopersicon species. I. Character definition and changes in gene expression

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Receieved: 31 December 1992 / Accepted: 4 January 1993

Abstract. Salt tolerance defined in terms of fruit yield under different NaCl concentrations (171.1 and 325.1 mM) is analyzed in 11 lines belonging to: *Lycopersicon esculentum*, *L. cheesmanii*, *L. chmielewski*, *L. peruvianum* and *L. pimpinellifolium*. Four *L. pimpinellifolium* lines and two *L. cheesmanii* lines tolerated the 171.1 mM treatment; the latter species even tolerates 325.1 mM of NaCl. Changes in gene expression induced by salt treatment were also investigated by studying anther and leaf zymograms for *L. esculentum* and one salt-tolerant *L. pimpinellifolium* line, and leaf proteinograms for all lines. Changes in leaf PRX and MDH enzymatic systems were detected, mainly in the salt-sensitive genotype (*L. esculentum*). Four salt-related peptides from 14 500 to 40 000 daltons were found. A polyclonal antibody raised against one of these peptides (number 2), also binds another peptide, named 2′, of much higher molecular weight, present both in control and salt-tolerant *L. cheesmanii* lines at the end of 171.1 mM treatment. The xero-halophyte shrub *Atriplex halimus* also showed a likely 2′-homologous peptide with this treatment, while its counterpart C_3 species *A. triangularis* did not.

Key words: Salt tolerance – *Lycopersicon* – Yield – Proteins – C_4 species

Introduction

Salinity is a major factor limiting agricultural production in large areas worldwide. The global extent of saline soils ranges between 400 and 950 million ha, and it has been estimated that one-third of the 230 million ha under irrigation is affected by salinity (Epstein et al. 1980). Salinity especially affects third world countries, forcing their people to migrate since the technology to combat it is extremely costly, requiring large expenditures of energy to reclaim land and maintain salt balances. On the other hand, these countries have been crucial for establishing germplasm bank collections; therefore, efforts have to be directed towards tailoring crop plants to suit more saline environments. Additionally, in highly developed countries like the USA, plant breeders use saline drainage water for crop production instead of disposing it because growers face increasing competition from urban and industrial water use (Kelman and Qualset 1991). Moderate salinity, however, can actually increase yields in crops like cotton, or else markedly improve the quality of tomato and melon fruits, while somewhat reducing the total yield (Shanon and Qualset 1984; Pasternak 1987; Gough and Hobson 1990).

In recent years an ever-increasing number of reviews and papers (Yeo 1983; Jones and Qualset 1984; Pasternak 1987; Yeo et al. 1990; Kelman and Qualset 1991; Saranga et al. 1992) have been published on the salt tolerance of plants and on crop production under saline conditions. Salinity is such a complex character that the field of specialization of the the authors necessarily biases their work which falls into four main research areas: soil and water management, from cell to whole plants physiology, change in gene expression, and plant breeding for salt tolerance. A considerable research effort is now being directed to this last approach to the problem.

The cultivated tomato is moderately sensitive to salinity (Maas and Hoffman 1977). Although some cultivars, such as Moneymaker and Edkawi, perform well in absolute terms under moderate saline treatments (Cuartero et al. 1992), relatively high salt tolerance was found in some wild *Lycopersicon* species: namely, *L. cheesmanii*, *L. pennellii* and *L. peruvianum* (Saranga et al. 1992).

Communicated by H. F. Linskens

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For a viable breeding program, it is necessary to identify characters which can be used as markers of salt tolerance. Ideally, such characters should be simple, precise, economical and measurable at early developmental stages. This would provide the possibility for indirect selection schemes that greatly reduce the number of plants on which salt tolerance has to be finally assessed. Cruz et al. (1990) evaluated 18 characters, mostly physiological, for ascertaining salt stress response in *Lycopersicon* species. To our knowledge, only the accumulation of proline and glycinebetaine (Jones and Qualset 1984; McCue and Hanson 1992), acting as non-toxic osmolytes in some species (barley, members of Chenopodiacea, such as sugar beet and spinach) in response to osmotic stress, are thought to contribute to drought and salinity tolerance (Wyn Jones et al. 1977). In these cases, the accumulation itself, or rather, the enzymes involved in such an accumulation, serve not only as markers but, at the very least, are part of the cause of salinity tolerance. For tomato breeding purposes, the objective of the present paper is to analyze the character of salt tolerance under different saline levels, and to look for possible genetic markers associated with it, in an initial screening of lines belonging to: *L. esculentum*, *L. cheesmanii*, *L. chmielewski*, *L. peruvianum* and *L. pimpinellifolium*.

Materials and methods

Eleven lines, kindly supplied by Drs. F. Nuez and C. M. Rick, were tested for their salt tolerance. The lines belong to the following species: *L. esculentum* cvs Edkawi and Madrigal, *L. peruvianum* (one line), *L. chmielewski* (one line), *L. pimpinellifolium* (lines named 1, 4, 5, 6 and 7) and *L. cheesmanii* (lines named 2 and 3). Four plants each of *Atriplex triangularis* (*hastata*) and *A. halimus*, collected in the Monegros desert (Spain), were also used for antibody tests.

Nine plants per line and treatment were grown on sand and irrigated with the following saline treatments:

(A) a one-half Hoagland solution used as a control, its conductivity was one deciSiemen per meter (1 dS/m).
(B) a control solution plus 171.1 mM of NaCl (conductivity of 15 dS/m).
(C) a control solution plus 325.1 mM of NaCl (conductivity of 30 dS/m).

The final concentration of NaCl for treated plants in B or C was obtained as follows: 1 month after germination the treatments began in a greenhouse with both photoperiod (12 h light) and temperature (25 °C ± 10 °C) control. The amount of NaCl was increased gradually every week (1, 4, 7, 10, 15, 20, 25 and 30 dS/m), until the final conductivity of the treatment was attained.

In a separate experiment, line 1 was also cultured under 1, 4, 10 and 15 dS/m, using nine plants per treatment.

Nine plants each of Madrigal and line 1 were also subjected to an additional saline treatment using 256.65 mM of NaCl (conductivity of 22 dS/m).

Only those lines that produced fruits at least under condition B were considered as salt-tolerant.

Three yield components were studied by a two-way ANOVA (lines × treatment): fruit number (FN), total fruit weight in grams (TW) and average fruit weight in grams (FW).

Leaf and anther isoenzymatic systems were studied using 12% starch-gel electrophoresis following the methods described by Bretó et al. (1992). Eight leaf enzymatic systems, EST, EP, SOD, PGM, SDH, PRX and GOT, were investigated in cv Madrigal and in line 1 (salt-sensitive and tolerant genotypes, respectively) under experimental conditions A, B and C. Eleven anther enzymatic systems, PGI, EST, GDH, TPI, GOT, SOD, ACO, PGM, MDH, 6PG and ME, were also investigated in cv Edkawi (salt-sensitive genotype) and line 1 under conditions A and B.

Proteins from control and treated plants were extracted from leaf tissue in 84 mM citric acid, 32 mM Na_2HPO_4 and 15 mM 2-mercaptoethanol, pH 2.8, buffer. SDS-polyacrylamide gel electrophoresis (the running gel was 19% acrylamide) was used to obtain proteinograms following the techniques described in Conejero and Semancik (1977).

A polyclonal antibody was raised in a 2 kg Californian × Neozelander rabbit against a peptide, named peptide 2, found to be differentially expressed in the mature leaves of line 1 under the condition B. This peptide was obtained by cutting the relevant piece out of the polyacrylamide gel and electroeluting it from this piece. Seven intravenous injections of 300 µg each were given on days 1, 10, 24, 35, 38 and 50, and a further injection of 600 µg on day 42.

Western blotting was performed in a Bio-Rad trans-blot cell, following the operating instructions provided, on Immobilon-P membranes. Western blots were blocked overnight in TBST (20 mM TRIS-HCl, 500 mM NaCl, pH 7.5 plus 0.5% Tween 20). The antibody against peptide 2 was used in a 1:250 dilution in TBST buffer and the anti-rabbit antibody, labelled with alkaline phosphatase, was also used in TBST buffer dilution of 1:4000. Both incubations were performed during 1½ h, washing the membrane three times after every step with TBST buffer. The staining method is described in Blake et al. (1983).

Results

When the 10 dS/m conductivity was reached, all plants of *L. chmielewski* subjected to treatment B died. The *L. peruvianum* line survived treatment B (as did the *L. esculentum* cultivars), but without yielding a single fruit. Since this line yielded no fruit under control conditions either, a self-incompatibility system must be acting as a confounding factor. Lines 1–6 tolerated the 15 dS/m treatment. Lines 2 and 3 even tolerated the 30 dS/m treatment. Since lines 2 and 3 were studied in a different experiment from lines 4, 5 and 6, no statistical comparison can be made between these two groups of lines. Means and confidence intervals for the line-treatment interactions of the characters FN, TW and FW are depicted in Fig. 1a for lines 1, 2 and 3, and in Fig. 1b for lines 1, 4, 5 and 6 (line 1 was included in both experiments as a control).

Regarding the yield characters of line 1 under the 1, 4, 7, 10 and 15 dS/m treatments, maximum FN was found at the 4 dS/m treatment which gave the only mean that was significantly different from the other

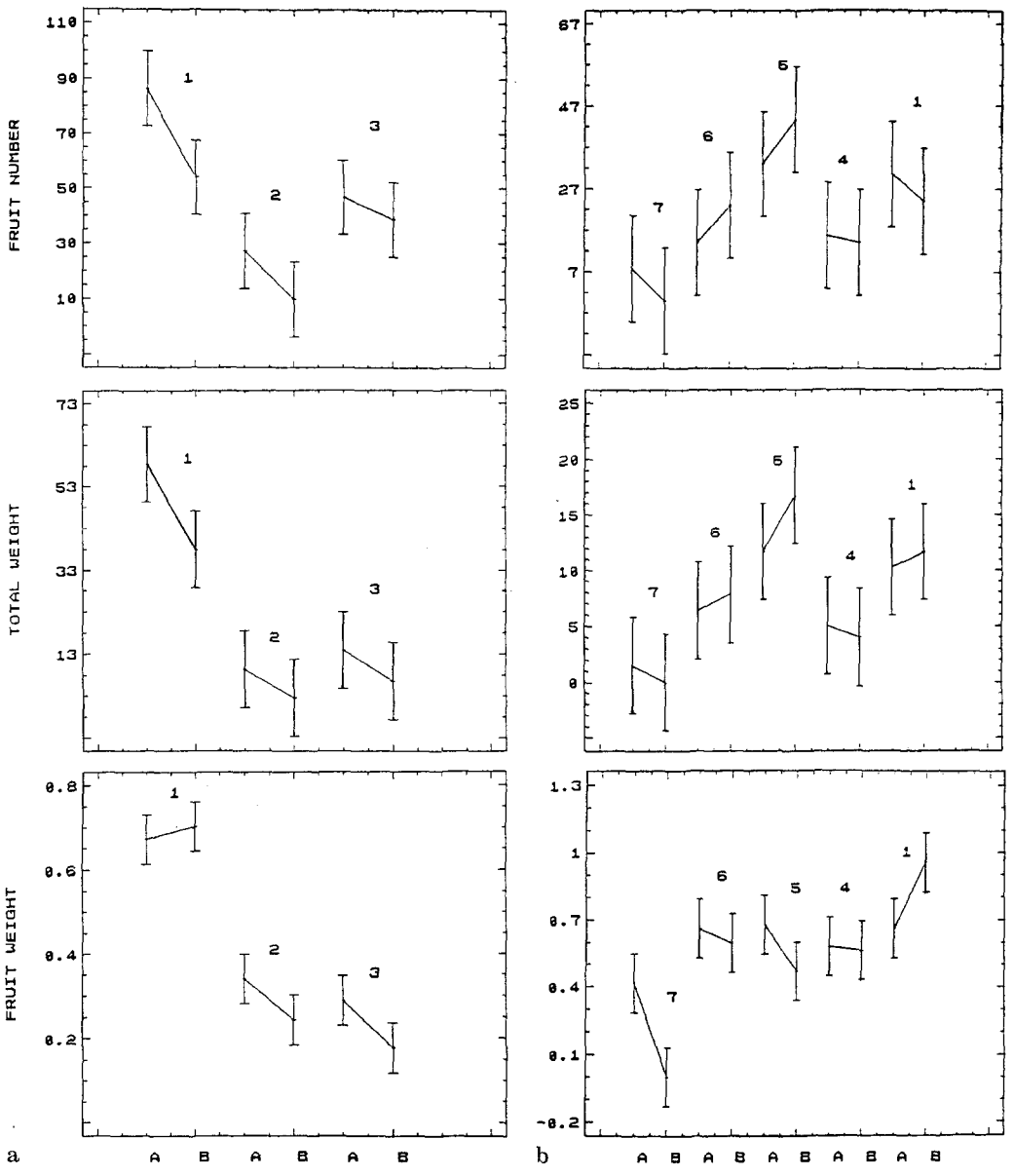

Fig. 1a, b. Line-treatment interactions for fruit yield traits. *Lines 1, 2 and 3* are presented in (**a**), and *lines 1, 4, 5, 6 and 7* in (**b**). *Line 7* which did not tolerate treatment **B,** has also been included

treatments. No significant differences were found for TW or FW.

In general, when proteinograms of control and salt-treated plants are compared, a decrease in the amount of most peptides is observed, some of them even disappearing. This is specially true for the 30 dS/m-treated plants (Fig. 2).

Four salt-related peptides were found. Their molecular weights range from 14 500 to 40 000 daltons. Peptide 2 has been found in lines 1, 4 and 6; peptide 3 in the Edkawi cultivar, and peptides 4 and 7 in lines 1, 4, 5 and 6. Therefore, all these peptides except 3 are present in salt-tolerant lines, although no salt-related peptide was detected in the *L. cheesmanii* lines (tolerant to the highest salinity level). All these peptides underwent a change in relative amount on the gel during treatment, the precise change depending on the line.

No difference in anther isozyme expression was observed. Differences in leaf isozyme expression was detected only in peroxidases and MDH (Fig. 3). The fastest migrating peroxidase, present only in Madrigal, decreased in staining intensity when NaCl concentration increased and was undectable in the 22 dS/m treatment. The slowest migrating MDH isozyme was not evident under the 22 dS/m treatment in either cv Madrigal or in line 1 and the next migrating isozyme

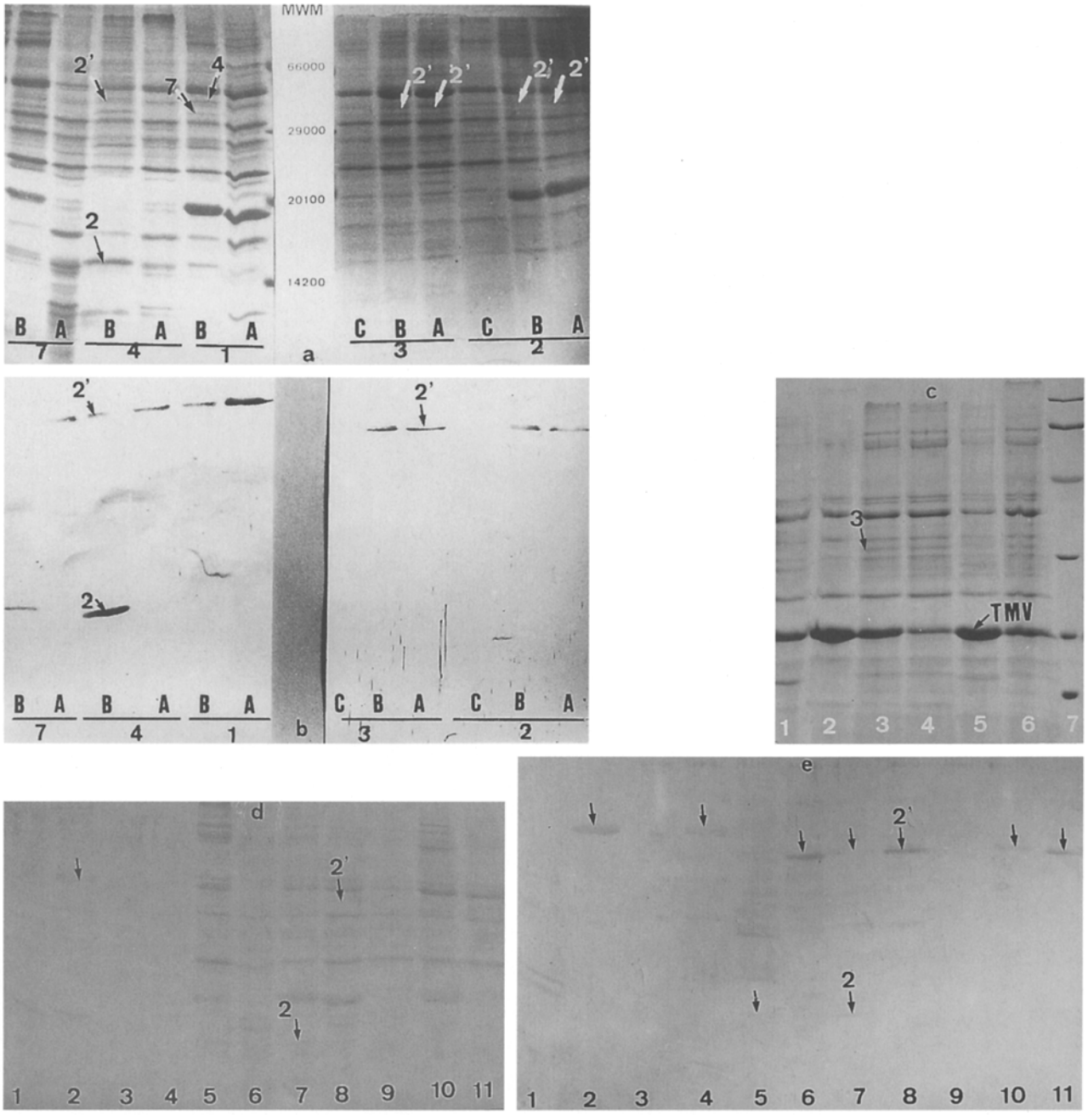

Fig. 2a–e. Salt-related peptides (*arrows*) on coomassi blue-stained gels (**a**, **c**, and **d**) and on Western blots after incubation with polyclonal antibody raised against peptide 2 (**b and e**). **a** *Numbers 1, 4, 7, 2 and 3* refer to the *Lycopersicon* lines; *A*, *B* and *C* to the treatments (see text). **b** Stained Western blots from gels in **a. c** Edkawi proteinograms: *lanes 1 and 2* are control (treatment A) plants, and *3–6* are salt-treated (treatment B) plants; molecular weight markers are in *lane 7* (97.4, 66.2, 42.7, 31.0, 21.5 and 14.4 kDa). **d** Stained gel after blotting: *lanes 4 and 2* are from *Atriplex halimus*, and *3 and 1* from *A. triangularis*; *lanes 11, 10 and 9* are from line 3; *8 and 7* from line 1; and *6 and 5* from line 7. *Lanes 11, 8 and 6* are from plants under control treatment A; *lane 9* from a plant under treatment C; and lanes *10, 7 and 5* from plants under treatment B. Except for *lanes 1 and 2*, leaf samples are from plants grown more than 3 months after treatment; *lanes 1 and 2* are from plants changed to control conditions for 1 more month. **e** Stained Western blot from gel in **d**

changed its relative mobility on the gel only in Madrigal.

Western blots containing control and treated plants were incubated with the polyclonal antibody raised against peptide 2. This antibody binds both peptide 2 and, unexpectedly, a peptide (number 2') of similar molecular weight (around 35 000 dalton) to peptide 4. In the control, as well as in salt-treated but

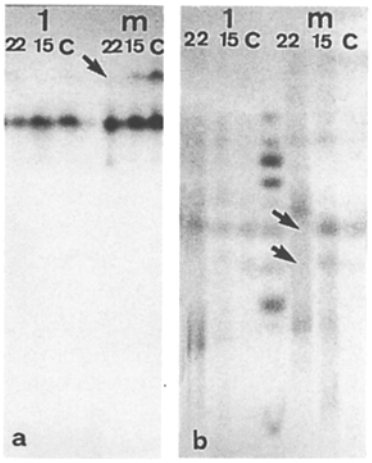

Fig. 3. Differences in leaf zymograms for anodal PRX (**a**) and MDH (**b**). *C*, *15* and *30* stand for control, 15 and 30 dS/m treatments, respectively; *1* and *m* stands for line 1 and Madrigal

not affected plants, only 2′ is immunologically detectable, while either no peptide or only 2 is detected in salt-affected plants. After long exposure (more than 3 months) to the 15 dS/m treatment, salt-tolerant lines 1, 4, 5 and 6 showed both bands (Fig. 2). The antibody clearly binds a peptide of higher molecular weight than 2′ on Western blots of the xerohalophyte *Atriplex halimus* cultured under 15 dS/m. This was not found in the other *Atriplex* species.

Discussion

Salinity is a very complex character and many authors have attempted to approach it from very different points of view. However, there are no examples of crop cultivars bred for salinity resistance that have proven to be commercially successful in saline ecosystems (Cuartero et al. 1992). Our results suggest that the main problem in this regard is to clearly define the character to breed for. The salt tolerance of young tomato plants is not well correlated with that of mature plants (Shannon 1979; Guerrier 1984; Norlyn and Epstein 1984). From an economic point of view, salt tolerance has to be defined in terms of fruit yield and not for the ability to grow. We have found that some genotypes (the cultivar Edkawi, for instance) can grow adequately under saline conditions but produce no fruits. This is an important drawback in using physiological characters of the vegetative component, while disregarding the fertility and fruit development process, to evaluate the salt tolerance of a plant where the fruit is the commercial product. Another aspect of the definition affects the term salinity; in the present paper we refer to increasing amounts of NaCl in the nutritive solution used for irrigation, but there are plenty of other saline conditions, including sea water dilutions, that affect the results. Moreover, the level of salinity is a crucial part of the definition. At a low salinity level (50 mM NaCl, for instance) most crop species, except those classified as sensitive by Maas and Hoffman (1977), have enough genetic potential to identify old cultivars, land races, etc., within the cultivated species that could be used as donors of salt tolerance. Additionally, Kelman and Qualset (1991) found that selection in low salinity environments (1–5 dS/m) may produce wheat cultivars with a high-yielding potential under environments with moderate salinity stress (around 7 dS/m). However, other authors (Richards et al. 1987; Saranga et al. 1992) found no relation between yields at low and high salinity levels (beyond 10–15 dS/m). Hence, under these conditions, donors of salt tolerance can not usually be found within cultivated species. At salinities above 50% of the concentration in sea water (around 23 dS/m for Mediterranean sea water) a halophyte is needed (Yeo et al. 1990).

After clearly defining the character to be the objective of the breeding program, the next problem is how to evaluate it by screening. Some plant breeders evaluate salt tolerance in terms of relative yield in comparison to control conditions (Richards et al. 1987). As shown in Fig. 1, the yield of lines 2 and 3 of *L. cheesmanii* does not change when the control and treatment are compared but, in absolute terms, the yield of line 1 of *L. pimpinellifolium* under treatment B is superior to the yields of the lines 2 and 3 under control conditions. Therefore, even though this line is more sensitive to salinity, it is commercially more desirable. In addition, the polygenic nature of the character itself makes the line-treatment interaction change from one experiment to another, as we have seen for line 1. Therefore, for the present experiments, we prefer to evaluate the material for its salt tolerance (i.e., yield) under a fixed salinity level in comparison with testers grown at the same treatment. Our testers were line 1 and the Edkawi and Madrigal cultivars.

If the salinity level was 30 dS/m there would be no other choice than to select lines 2 or 3 as donors for salt tolerance. However, at 15 dS/m, the absolute yield, and the fact that *L. pimpinellifolium* is the closest related species to *L. esculentum* (Bretó et al. 1992), led us to choose lines 1 and 5 of *L. pimpinellifolium* as donors for tolerance to this salinity level. Recently, Cuartero et al. (1992) have found halophytic characters in *L. pimpinellifolium* that support our conclusion.

In order to identify characters that could be used as markers of salinity tolerance in tomato breeding programs, changes in gene expression which occur during salt treatments were studied by analyzing leaf and anther zymograms and leaf proteinograms. Genes whose expression is increased during the stress situation are presumably critical to the adaptation of the organism to adverse conditions; thus, an examination of the genes which are

activated in response to stress may prove useful in understanding the biological response of plants to stress and may point the way to new and valuable goals for agriculture (Matters and Scandalios 1986). On the other hand, it is possible that the tolerant response is, at least in part, a consequence of overcoming enzymatic inactivation, in which case we would have to look for "salt tolerant proteins". In some cases, changes in specific genes have been identified; however, in most cases, the functional identity of stress-induced genes is unknown (Matters and Scandalios 1986). Bretó et al. (1992) found that the cultivar Edkawi is characterised by several alleles at the *Tpi2*, *Got2* and *Pgm2* loci that are also characteristic of *L. pennellii* and *L. cheesmanii*, and others at the *6Pg2* and *Mdh* loci that are characteristic of *L. pennellii*. These genes are good potential candidates as genetic markers of salt tolerance in breeding programs where Edkawi is used as the donor. The same could be said about line 1 and its rare allele at *Aco1* which is also present in *L. pennelli*. We have found no change in anther and ovary isozyme expression at 15 or 22 dS/m treatment (assayed only in Edkawi and line 1); here, apparently, enzymes and metabolism both seem to operate as in control plants, even in the Edkawi cultivar that yielded no fruit under the salinity treatments. Thus, we think that it could be a fruit development problem rather than one of fertility. An effect of salinity stress has been found on ribonucleolytic activities (Rouxel et al. 1989), on enzymes of carbon metabolism during the induction of Crassulacean acid metabolism (Holtum and Winter 1982), on acid phosphatases (Pan 1987), betaine aldehyde dehydrogenase (McCue and Hanson 1992), MDH, catalase, peroxidase and SOD (Kalir and Poljakoff-Mayber 1981) in leaves from very different plant species. From our results on leaf isozymes, we have shown that NaCl affects only the MDH and PRX systems. These isozymes appear to be salt sensitive. Moreover, the salt-sensitive genotype is clearly the most affected. Therefore, these changes should be studied more thoroughly because, apart from providing good markers for salinity tolerance, they may also contribute to a possible understanding of the salinity tolerance or sensitive response itself.

The induction of specific mRNA and proteins in response to salt stress have been described for different biological systems. So far, the functions or processes in which these proteins are involved are unknown, although it is assumed that they are essential to plant survival under conditions of water deficit. In *L. esculentum* three main salt-induced proteins have been identified; osmotin, whose molecular weight is around 26 000 daltons (Singh et al. 1987; King et al. 1988), and which can also be found in control plants at some developmental stage, TAS14 of 14 000 daltons (Torres-Schumann et al. 1991), and TSW12 whose molecular weight is 12 000 daltons and is probably a lipid transfer protein (Torres-Schumann et al. 1992). The present paper describes a peptide (number 2) of 14 500 daltons which is salt induced in most *L. pimpinellifolium* lines at different stages of salt treatment. An other peptide of 35 000 daltons (number 2'), that reacts immunulogically as does 2 against the same antibody, is present in control plants. The more salt tolerant the genotype, the longer this peptide lasts before disappearing after salt treatment. At the end of treatment B only the *L. cheesmanii* lines and the xerohalophyte shrub *A. halimus* showed peptide 2' and its likely homologue of higher molecular weight, respectively. Most *Atriplex* shrubs are characterised by C_4 photosynthesis, whereas the herbaceous *A. triangularis* is a C_3 species. C_4 species show a more efficient fixation of CO_2, and an efficient use of water and nitrogen; however, NaCl can shift the balance from C_3 to C_4 photosynthesis in some species (many C_4 species are adapted to growing in saline environments). $NADP^+$ malic dehydrogenase, pyruvate Pi dikinase and PEP carboxylase have been suggested as the most likely regulatory enzymes for leaf photosynthesis (Ray and Black 1979). Further investigations are needed, however, before concluding that an association exists between peptide 2', a MDH isozyme, or a PRX isozyme, with the salinity tolerance response.

Acknowledgements. We thank Drs. F. Nuez and C. M. Rick for providing the *Lycopersicon* lines and Drs. M. J. Ochoa and M. A. Cambra for providing the *Atriplex* plants. We are also grateful to Ms. Ana Sanchis and Mr. F. Bimbo for technical assistance. This work has been partially funded by grants from INIA and CEE (M.J.A.) and Conselleria de Cultura, Educació i Ciencia (M.P.B.).

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