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Genotypic Responses to Salinity

DIFFERENCES BETWEEN SALT-SENSITIVE AND SALT-TOLERANT GENOTYPES OF THE TOMATO[1,2]

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ABSTRACT

Four ecotypes of the species *Lycopersicon cheesmanii* ssp. *minor* (Hook.) C.H. Mull. from the Galapagos Islands were compared with *L. esculentum* Mill cv. VF 36 with respect to salt tolerance. The *L. cheesmanii* ecotype that proved most salt-tolerant was selected for detailed comparison with the *L. esculentum* cultivar. Plants were grown in modified Hoagland solution salinized with synthetic seawater salt mix. Growth rates under saline conditions were examined and amino acid, sugar, total amino nitrogen, free acidity, and Na and K levels in the tissues of the most and least tolerant plants were measured under salt stress and nonstress conditions. Results indicate that all Galapagos ecotypes were far more salt-tolerant than was the *esculentum* cultivar. They could survive in full strength seawater nutrient solution while the *esculentum* cultivar could not in most cases withstand levels higher than 50% seawater. Growth rates were reduced in both species under saline conditions but the *esculentum* cultivar was more severely affected. High levels of total amino nitrogen, specific amino acids, and free acidity along with low sodium content were found in the salt stressed VF 36 cultivar. The opposite responses were noted in the salt stressed treatments of the Galapagos ecotype. Tissue sugar levels did not appear to be similarly correlated with salt stress in either species. Potassium content fell sharply during salinization in the Galapagos ecotype while in the *esculentum* cultivar it declined relatively little even at high levels of salinity.

Almost two decades ago, Bernstein and Hayward (1) wrote: "An understanding of the physiology of salt tolerance of plants is important for an effective approach to the salinity problem, which is of increasingly widespread occurrence." Coupling an understanding of the genetic control of salt tolerance with this physiological approach adds the further dimension of promising to lead to the development of salt-tolerant crops (4, 5). It is axiomatic in modern physiology and biochemistry that specific capabilities of organisms depend on the synthesis of appropriate enzymes, this synthesis in turn being gene-controlled. Assuredly, the specific capabilities possessed by those plants able to tolerate saline conditions fatal to other plants are no exception to this generalization. Several authors have drawn attention to genotypic differences between salt-tolerant and salt-sensitive plants in respect to a number of pertinent physiological and biochemical parameters (2, 5, 9, 13). It is becoming evident that the combined tools of the plant physiologist, geneticist, and breeder must be brought to bear on the increasing salinity problems confronting irrigation agriculture on a worldwide scale. Furthermore, if strains of crops capable of coping with seawater or brackish water salinity could be generated, what is now a problem could become a vast opportunity for crop production by tapping the immense wealth of water and mineral plant nutrients of the oceans without the energy-costly process of industrial desalination.

The experiments reported here represent a contribution to this approach. Two species of the tomato, one salt-tolerant, the other salt-sensitive, were compared under saline and nonsaline conditions in regard to a number of physiological and biochemical features. The two species differed markedly in respect to several such characteristics. Because the two species are interfertile, they offer the opportunity both for comparative studies like those reported here, and for a program of breeding for salt tolerance.

MATERIALS AND METHODS

Variation in Salt Tolerance. Seeds of *L. cheesmanii* ssp. *minor* (Hook.) C.H. Mull. were soaked in 1.3% NaOCl solution for 70 min to dissolve the outer coat, a necessary procedure for germinating seeds of this species (11). They were then rinsed in tap water for 30 min followed by 30 min in 5 mM $CaSO_4$ to remove residual NaOCl. Seeds of four ecotypes of this species were then placed on stainless steel grids covered with boiled cheesecloth on 3-liter containers of half-concentration modified Hoagland solution (5).

These were placed in the dark, and the solutions were aerated for 5 days at 23 ± 1 C. They were then transferred to a regulated growth chamber under conditions of 14 hr of light at 28 C and 10 hr of darkness at 20 C. Seeds of *L. esculentum* Mill cv. VF 36 were planted in a similar manner without the NaOCl treatment 5 days later, because in germination and early development the *cheesmanii* ecotypes are slower than the VF 36 cultivar. When the plants were 22 and 17 days old, respectively, each seedling was wrapped in Dacron batting at the hypocotyl and placed in the central hole of a cork stopper. These were placed in the covers of 100-liter tanks of aerated 0.1 modified Hoagland solution, 10 plants per tank. The experiment was conducted in the greenhouse from early January through mid-April. The daytime temperature averaged 27 C, and the night temperature 21 C. Each treatment was salinized with 0.1 seawater increments every 6 to 8 days beginning on the 7th day after transfer to the greenhouse. This was accomplished by the addition of 330 g of dried, finely ground synthetic seawater salt mix (Rila Marine Mix, Rila Products, P.O. Box 114, Teaneck, N.J. 07666). The salts were added by removing 4 liters of solution from each tank and dissolving the mixture in it, half in the

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[2] This paper is affectionately dedicated to Leon Bernstein. He has earned his salt.

morning and half in a similar fashion in the afternoon. Salinization was split into two additions to minimize physiological shock to the plants. This process was continued until all the plants in a treatment had died or until full seawater concentration was reached. Full seawater concentration was defined by the criteria of an electrical conductivity of 56 mmhos/cm and a Na concentration of 460 mM. Nutrient levels in the solutions were monitored by analyzing K content. Both Na and K were determined by flame photometry. Solutions were renewed when K levels fell below 0.1 mM. Progress was recorded by measuring plant growth in terms of vigor, leaf color, relative growth rate, general appearance, survival, and 35-mm color slides for visual comparison at 10-day intervals. The experiment was terminated after 103 days at which time the surviving plants had been subjected to full seawater concentration for 12 days.

Growth Comparisons. Germination and planting procedures were similar to those listed above. In this series 42-liter tanks of 0.2 concentration modified Hoagland solution were used with six plants per tank. Each of the four Galapagos ecotypes and the *esculentum* cultivar were grown in replicate: one treatment as an unsalinized control, the other being salinized to 0.2 seawater at two 0.1 seawater increments spaced a week apart by the addition of 141 g of dried ground seawater salt mix. This gave a final concentration of approximately 90 mM NaCl in the nutrient solution. Growth rate comparisons were made by recording plant height above the container top, individual canopy diameter, and fresh weight comparison at harvest. The experiment was terminated at 64 days, 38 days after salinization to 0.2 seawater. It was conducted from mid-January to the end of March.

Amino Nitrogen and Free Acidity. Germination, planting, and salinization procedures were similar to those given earlier. Salinization was continued up to 0.4 seawater. Plants of the most salt-tolerant Galapagos ecotype (1401) as determined earlier and the *esculentum* VF 36 were grown in replicate. One set of six plants of each species was designated as the control while the other was salinized as described earlier. Composite samples consisting of the youngest mature petioles and leaves were taken from the plants of each set at levels of 0.3 and 0.4 seawater concentrations 6 days after each salinization. Controls were similarly sampled at the same time. Fresh weights were taken and the tissue placed in a draft oven and dried at 68 C for 48 hr. Dry tissue samples were ground in a Wiley mill and amino nitrogen and free acidity were determined for the controls and salt-stressed tissues using the Sorenson method (6). All determinations were done in triplicate. This experiment was conducted from early July through the end of August.

Amino Acids. Germination, planting, and salinization procedures were similar to those given above. The 0.5 modified Hoagland solutions were salinized to the level of 0.3 seawater. Tissue samples from both stressed and control plants were taken on the 58th day of the experiment after allowing the plants time to adjust to this salinity level. The experiment was conducted from mid-April through early June. Plants were transported from the greenhouse into the laboratory where they were rinsed in distilled, demineralized H_2O. Root, petiole, and leaf tissues were then excised and immediately transferred to a cold room at 4 C. Leaves were separated from the petioles and all tissue samples placed in ether kill jars for 20 min before juice extraction. Juice extracts were done by placing 2 g of tissue in 20-cm pieces of 1.5-cm diameter Tygon tubing clamped at one end. The samples were then crushed inside the tube and the juice extract collected. A small amount of phenylmercuric nitrate was added to each extract as an antibacterial agent. Determinations of amino acids were made using 20-μl aliquots of concentrated amino acid extract standards applied to 46 × 57 cm Whatman No. 1 chromatography paper. Amino acids were separated by a two-dimensional descending method. The first solvent system consisted of 1-butanol-acetic acid-water (12:3:5). The second was phenol-water (5:1). The chromatograms were developed in 0.5% ninhydrin in acetone and heated at 100 C for 10 min. Qualitative determinations were made by comparing the size, location, number, and color intensity of the spots with the known standards. Comparative examinations were made in natural, artificial, and UV light.

Sugar Analysis. Sugar analyses were done on the juice extracts obtained for the amino acid assay described earlier. Determinations were made using 20 μl of the juice extracts cochromatographed with 10 μl of 2% solutions of sucrose, glucose, xylose, ribose, and fructose. The solvent used was ethyl acetate-pyridine-water (8:2:1), 90 ml per sheet. Run time was 18 to 20 hr in saturated tanks. Development was with 0.5% orcinol and 15% trichloroacetic acid in isopropyl alcohol for the ketose sugars and 2% aniline and 2% trichloroacetic acid in ethyl acetate for the aldose sugars. Drying and examination were similar to the amino acid assay. Comparison was done by assigning numbers on a scale of zero to five to the developed spots according to intensity and size, the standards being designated as five. Approximate quantitative comparison could then be made.

Electrical Conductivity. Electrical conductivity measurements were made on the juice extracts of combined petiole and leaf tissue obtained from the same plants used in the amino acid determination. Nutrient solutions from the control and salinized treatments were also measured. Juice extracts and salinized nutrient solutions were diluted 1 to 100 and electrical conductivity was measured using an electrical conductivity meter. No dilution was necessary for the control nutrient solution.

Sodium and Potassium Analysis. Tissue samples were taken at various salinity levels from plants grown using the procedures listed earlier. The youngest mature petioles and leaves were taken and dried in a draft oven at 68 C for 48 hr. The tissue was ground in a Wiley mill and 0.5-g samples were ashed as described by Johnson and Ulrich (7). Na and K were determined by flame photometry.

RESULTS

Salt Tolerance. Plants of all four ecotypes of the Galapagos species were able to withstand seawater at full concentration (Table I). These ecotypes represented saline coastal, interior midlands (20-m elevation), and montane (1500-m elevation) habitats. All plants of the *esculentum* cultivar died when the salt concentration reached 0.5 seawater. All plants exhibited lower growth rates and a slightly darker green color at moderate salt concentrations than the controls. As the salinity levels increased differences began to emerge. The coastal 1401 and midlands 1044 ecotypes of the Galapagos species began flowering at 0.5 seawater, and continued to grow and flower up through 0.8 seawater. The coastal 1400 and the montane 926 Galapagos ecotypes showed less vigor. As the salinity levels increased above 0.4 seawater the lower petioles and leaves of the Galapagos species became chlorotic and eventually ab-

Table I. *Survival Rates of Four L. cheesmanii Ecotypes and VF 36 Cultivar of L. esculentum when Grown in Nutrient Solutions Salinized to Full Seawater Salinity*

Designation	Type	Survival
		%
1400	Coastal	40
1401	Coastal	90
1044	Midlands	90
926	Montane	50
VF 36	Cultivar	0

scised. This also occurred in older tissue under nonstress conditions, but the rate increased at the higher salinity levels. The older mature tissue became increasingly chlorotic at levels above 0.7 seawater long before it abscised, while new growth remained dark green and quite turgid. Survival rate of the 10 plants in each treatment in full seawater is given in Table I. Of the Galapagos species the coastal ecotype designated 1401 appeared to have the highest degree of salt tolerance.

Growth Comparisons. All of the salt treatments exhibited decreased growth when compared with similar unsalinized controls (Table II), but there were obvious differences in appearance between the two species. The Galapagos ecotypes became slightly darker in color than their respective controls but were still fairly vigorous with little overall indication of salt toxicity.

Table II. *Growth Comparisons of Four L. cheesmanii Ecotypes and VF 36 Cultivar of L. esculentum*

Data show growth in control and salinized nutrient solutions, 38 days after the 0.2 seawater concentration was reached.

Designation	Control	0.2 Seawater	
	g fresh wt/plant		*% of control*
1400	395	120	30.4
1401	375	110	29.3
1044	440	110	25.0
926	400	70	17.5
VF 36	390	60	15.4

Table III. *Amino Nitrogen and Free Acidity in Leaf Tissue of 1401 L. cheesmanii Ecotype and VF 36 Cultivar of L. esculentum under Control and Salinized Conditions*

Treatment	Amino N	Increase	Free Acidity	Increase
	% dry wt	*% over control*	*meq/g dry wt*	*% over control*
1401				
Control	0.32		0.21	
0.3 Seawater	0.38	19	0.27	29
0.4 Seawater	0.41	28	0.28	33
VF 36				
Control	0.38		0.27	
0.2 Seawater	0.69	82	0.40	48
0.4 Seawater	0.56	47	0.41	52

The *esculentum* cultivar became chlorotic and developed symptoms similar to Mg deficiency as described by Epstein (5). In addition to reduced growth and vigor the plants took on a generally unthrifty, spindly appearance with time. Differences among the Galapagos ecotypes were small at this low salinity level but again the coastal 1401 ecotype appeared most promising for further comparative experiments contrasting salt tolerance between these two species, and it was therefore used in further comparative experiments described below.

Amino Nitrogen and Free Acidity. Total amino nitrogen was 82% higher at 0.3 seawater concentration than in the unsalinized control for cv. VF 36. The corresponding value for the 1401 ecotype was 19% under the same conditions. Free acidity increased 49% above the control in cv. VF 36 and 29% under the same conditions in the 1401 ecotype. Both amino nitrogen and free acidity continued to increase at 0.4 seawater concentration, but the data for the cv. VF 36 may not be as reliable because the plants were suffering from the stress. See Table III for results.

Amino Acids. In the control treatments, amino acid content of the leaves and petioles of the 1401 ecotype was approximately equal to that of the cv. VF 36, but in the roots both the number of amino acids and their concentrations were higher in the 1401 ecotype. At the level of 0.3 seawater, however, the cv. VF 36 appeared to accumulate much higher levels in all tissue samples while the 1401 ecotypes showed only slight increases at this salinity. Prominent amounts of aspartic acid accumulated in all but one of the salt treatments in both species. The exception was in the leaves of the 1401 ecotype in which no aspartic acid could be detected. It was not detected in any of the control plants of either species. See Table IV for a listing of amino acids found in the various treatments of both species.

Sugars. Sugar levels tended to be lower in both species under salt stress when compared with the unsalinized controls, except for fructose which did not appear to be affected by the salt treatment in the VF 36 cultivar. Fructose levels in the 1401 ecotype tissue decreased under similar salinization. No other clear patterns emerged between the two species differentiating their responses to salinity with regard to sugar concentration. Dominant sugars under both salt stress and nonstress conditions were glucose and fructose; small amounts of xylose, ribose, and mannoheptulose were also present. No sucrose was found in any of the tissues assayed. See Table V for complete results.

Electrical Conductivity. Under salt stress conditions, the juice extracts of the 1401 ecotype had more than twice the number of charged ion species than did the extracts of the cv. VF 36, as

Table IV. *Amino Acids Found in Tissues of the 1401 L. cheesmanii Ecotype and VF 36 Cultivar of L. esculentum under Control and Salinized (0.3 Seawater) Conditions*

Treatment	Gly	Gln	Glu	γ-Amino butyric Acid	Val	Pro	Leu	Ser	Unknown	Asp
1401										
Control leaf	X	X	X	X	X		X		X	
Salt leaf	X	X	X	X	X		X		X	X
Control petiole	X	X	X	X	X		X			
Salt petiole	X	X	X	X						X
Control root	X		X	X	X		X			
Salt root	X	X	X	X	X	X	X	X		
VF 36										
Control leaf	X		X	X	X		X	X	X	
Salt leaf	X	X	X	X					X	X
Control petiole	X	X	X	X	X					
Salt petiole	X	X	X	X		X			X	X
Control root			X	X						
Salt root			X	X	X	X	X	X	X	X

Table V. *Quantitative Estimation of Sugars in Tissues of the 1401 L. cheesmanii Ecotype and VF 36 Cultivar of L. esculentum under Control and Salinized (0.3 Seawater) Conditions*

Treatment	Glucose	Fructose	Xylose	Ribose	Mannoheptulose (no standard)
	mg/g fresh wt				
1401					
Control leaf	8	12	0.4	0.4	Present
Salt leaf	2	2			
Control petiole	4	0.8			
Salt petiole	0.4	0.4			
Control root	2	4			
Salt root	0.4	0.4			
VF 36					
Control leaf	8	16			Present
Salt leaf	1	16	Trace	Trace	Present
Control petiole	6	0.8			
Salt petiole	2	0.8		Trace	
Control root		2			
Salt root	4	2			

determined by measurements of the electrical conductivity. The electrical conductivity of the 1401 salt treatment was 29 mmhos/cm compared with 14 mmhos/cm for the 1401 control. The cv. VF 36 salt treatment reached 14 mmhos/cm, with 10 mmhos/cm for the unstressed control. The juice extracts of the cv. VF 36 plants in the salt treatment had lower concentrations of charged ion species than did the solution in which the plants were grown. The electrical conductivity of the salt solution was 16 mmhos/cm compared with 1 mmho/cm for the control solution.

Sodium and Potassium Levels. Consistently in a number of experiments, leaf Na levels remained low in the cv. VF 36 under conditions of increasing Na concentrations in the nutrient solutions, up to a point. Beyond this point, usually in the vicinity of 0.5 seawater concentration, leaf Na levels increased sharply and the plants died. In the 1401 ecotype, Na content in the leaves increased with each increase in the nutrient solution. Figure 1 summarizes the results of several experiments. It appears that the cv. VF 36 tends to exclude Na from the leaf tissue, to which it is toxic, while the 1401 ecotype freely accumulates Na in the leaf with no similar toxic effects. Potassium levels in the cv. VF 36 remained high in the tissue, indicating that K was being selectively accumulated even at these high Na solution levels where the Na/K ratio was greater than 75/1. Potassium content decreased sharply in the 1401 ecotype as the Na levels increased, indicating that no comparably effective selective mechanism was present or apparently necessary for survival at these salinity levels. See Figure 2 for details.

DISCUSSION

There appeared to be a marked difference in the ability of these two species to deal with saline environments. All of the Galapagos ecotypes were similar in their high tolerance of salinity, compared with the relatively low tolerance of the VF 36 cultivar. The selection of the 1401 coastal ecotype as the representative of the contrasting species for the later experiments was made after consideration of survival rates and vigor at the higher salinity levels along with its history of survival in a naturally saline environment and its ability to complete its life cycle under saline conditions. Original seed stock was taken from a plant growing on a coastal bluff a few meters from the high tide line (10).

All of the Galapagos ecotypes as well as the cv. VF 36 exhibited reduced growth rates under mild salt conditions, indicating that neither species was benefiting from nor requiring Na in more than micronutrient concentrations. Osmotic effects may also contribute to the low growth rates under saline conditions (3). Their physical characteristics under salt stress were, however, quite different in that the Galapagos ecotypes exhibited drought-like stress while the cv. VF 36 appeared to show toxicity symptoms, especially after being exposed to moderate concentrations of NaCl (0.2 seawater) for an extended period of time. Whether these symptoms were brought about by Na, Cl, or other constituents in the seawater is not known, but they were very similar to the symptoms exhibited when only NaCl was used to salinize the solutions in other experiments, thus reducing the likelihood that they were caused by other potentially toxic ions in the seawater salt mix.

Total amino nitrogen and free acidity analyses were performed to ascertain whether there were differences between these species under salt stress and nonstress conditions, and to note any correlation between the levels of these organic solutes

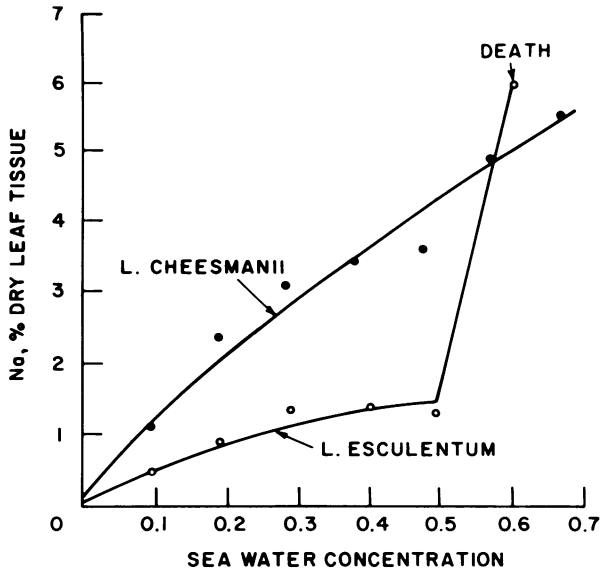

FIG. 1. Percentages of sodium in dry leaf tissue as a function of the salinization of the nutrient solution with seawater salt mix.

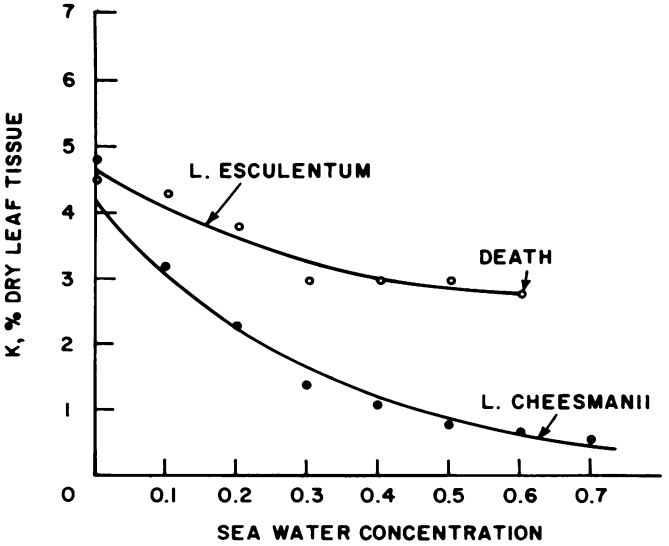

FIG. 2. Percentages of potassium in dry leaf tissue as a function of the salinization of the nutrient solution with seawater salt mix.

and salt tolerance in terms of a mechanism for maintaining a low water potential in the plant, as is necessary for survival in saline environments (5, 8). The results indicated that the cv. VF 36 increased its concentrations of both total amino nitrogen and free acidity to a greater extent than did the 1401 ecotype under similar stress conditions. The mechanisms whereby salinity provoked the synthesis of these solutes are unknown. The increases of these solutes in the 1401 ecotype were considerably less, possibly indicating that the stress was being dealt with by other mechanisms (see below).

Specific amino acid analysis was performed in an attempt to discern if there was a build-up of any particular amino acid that might suggest a pathway or metabolic function that was being affected by the salt stress. Such analysis might also reveal markers for establishing tests for salt tolerance. Proline has been found to be such a marker in salt-tolerant plants exposed to salt stress. For a pertinent discussion and further references, see Stewart and Lee (12). Again the cv. VF 36 had higher concentrations though not necessarily a higher number of species of amino acids than did the 1401 ecotype under stress conditions in leaves, petioles, and roots. The most outstanding difference between salt stressed and nonstressed treatments for both species was the build-up of sizable concentrations of aspartic acid not found in any of the controls of either species. Since this build-up occurred in both the sensitive and tolerant species it would serve only as an index of salt stress but would not give any clues as to their relative tolerance to that stress.

Sugar analyses were performed in order to ascertain if there was a similar build-up of sugars under salt stress conditions as another possible means of dealing with low water potentials of saline environments. The results indicated that sugar levels decreased in both species under salt stress, and that there were no distinguishing differences between them that could be used as keys to salt tolerance.

Electrical conductivity measurements of juice extracts revealed that the 1401 ecotype contained over twice the number of charged ion species that the cv. VF 36 did under salt stress conditions, giving a clue to its means of dealing with salinity. The 1401 ecotype juice extracts had nearly twice the electrical conductivity of the salinized nutrient solution they were being grown in, while the electrical conductivity of the cv. VF 36 extracts was less than that of the salinized nutrient solution, with organic solutes in the tissue presumably making up the difference necessary for osmotic water absorption.

Leaf analysis for Na and K revealed that the cv. VF 36 tended to exclude Na from the leaf tissue while the 1401 ecotype accumulated sizable amounts of Na without being severely affected and without apparent toxicity. Potassium analysis indicated that the cv. VF 36 was highly selective in distinguishing between Na and K in the salt treatment because K levels remained at "luxury" concentrations even as the plants were dying. The 1401 ecotype showed no such distinction inasmuch as K levels dropped to values well below 1% of the dry weight while Na concentrations increased in the tissue. (Potassium concentrations as low as these are often considered indicative of actual or incipient K deficiency.)

From this it appears that the inability of the cv. VF 36 to withstand salinity is linked to its limited efficiency in keeping Na in the leaf tissue below toxic levels and compensating for the lower water potentials associated with salinity by increasing tissue levels of organic solutes, including amino acids. The 1401 ecotype is not similarly affected by Na and accumulates large concentrations (up to 7%) in the leaf tissue, as has been shown for other tomato genotypes (13). It appears that the plant shows a very limited ability to discriminate between K and Na in the transport of the two elements. This, coupled with the low toxicity of Na to this genotype, may allow Na to contribute to lowering the water potential in the leaf cells. Possibly, Na in the 1401 ecotype also substitutes for K in metabolic functions which, in the VF 36 cultivar, absolutely require the participation of K.

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