$$v_o = \frac{V_{max}.[S]}{k_m + [S]} \quad \text{for steady state;}$$

$$k_2 = \frac{V_{max}}{[E]_t} \qquad V_{max} = k_2.[E]_t$$

where S = substrat (external concentration of phosphate), E = enzyme (phosphate carrier), P = product (internal concentration of phosphate), ES = complex enzyme-substrat, k = constant of velocity, k_s = dissociation constant of the complex ES, k_m = Michaelis-Menten constant, v_o = initial velocity of the reaction between E and S, V_{max} = maximal velocity, k_2 = turnover of the enzyme (carrier), $[E]_t$ = total concentration of the free enzyme (carrier).

Cooperative kinetic:

Hill equation:

$$\frac{V}{V_{max}} = \frac{[S]^n}{k' + [S]^n}$$

$$K' = K^n{}_s.(a^{n-1}.b^{n-2}.c^{n-3}...z^1)$$

$$[S]_{0.5} = \sqrt[n]{K'}$$

$$R_s = \frac{[S]_{0.5}}{[S]_{0.1}} = \sqrt[n]{81}$$

where n = number of ligation sites for the substrat on the molecule of enzyme (carrier) = n_H = Hill coeficient; K_s = dissociation constant for each site; a, b, c...z = interactions factors between the differents sites; $[S]_{0.5}$ = half saturation of the sites; R_s = cooperativity index

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SALINITY AND MINERAL NUTRITION EFFECTS ON GROWTH AND ACCUMULATION OF ORGANIC AND INORGANIC IONS IN TWO CULTIVATED TOMATO VARIETIES

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ABSTRACT: A trial was conducted on the effect of salinity and method of fertilizer application on two varieties of cultivated tomato, *i.e.* VF 145 and Edkawi. Salinity ranged from 0.52 to 11 dS/m, and fertilizer was applied by either broadcasting in small doses or added with irrigation water. Weight of shoots, fruit yield, and sodium (Na), calcium (Ca), chloride (Cl), free proline contents in both developing and mature leaves, and total soluble salts and ascorbic acid contents in fruits were taken as evaluating criteria. Salinity depressed both growth and fruit yield, and simultaneously increased ion concentration in plant leaves. Sodium and Cl accumulated with salinity, being greater in mature leaves, while proline accumulation in developing leaves was much higher than in mature leaves. Total soluble salts and ascorbic acid were not affected. Liquid fertilization resulted in higher fruit yields than that obtained with the solid fertilizer treatments as well as better alleviating the depressive effects of salinity on plant growth and yield, especially at the lower salinity level where it was more beneficial to fruit yield. The VF 145 tomato variety was found a bit more sensitive to salinity than the Edkawi variety, and was affected differently by salinity, regarding both the yield and the pattern of organic and inorganic ion accumulation. Our results suggest that there exists a physiological mechanism that is involved in the salt tolerance difference observed between the two varieties that needs to be investigated.

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INTRODUCTION

Plants grown under saline conditions cope with salinity through three main mechanisms: avoidance, exclusion of salts, and by physiological tolerance which involves compartmentation and osmotic adjustment using organic and inorganic compounds (Greenway and Munns, 1980). However, there are quantitative differences among plants in the degree of response to salt stress (Epstein, 1985). This degree of response expresses salinity tolerance (Maas and Hoffman, 1977), while the capacity to accumulate excess solutes expresses the "osmotic adjustment" (Turner and Jones, 1980). This osmotic adjustment is supposed to reduce water potential in plant cells in order to maintain the flow of water into the plant.

A number of organic and inorganic compounds are reported to accumulate in salt-affected tissues according to Munns et al. (1982). Proline is reported to be one of these solutes (Stewart, 1981). Its amount varies with salinity (Buhl and Stewart, 1983). The interpretation of this response has varied from its description as a useful criterion for the selection of varieties suited to arid areas (Aspinall and Paleg, 1981) to nothing more than a measure of the rate of senescence (Hansen et al., 1977). Choosing between these controversial interpretations needs a reassessment in a more global sense. Thus, the knowledge of the metabolism and nutrition of plants may afford clues as to an understanding of the genetics of salt tolerance (Tal, 1985).

The purpose of our study is to examine salt tolerance among two tomato varieties that are different in their origin in relation to their patterns and extent of organic and inorganic solute accumulation in their leaves when stressed by salinity.

MATERIALS AND METHODS

This study was carried out in the 1986 season at the Soil Salinity Laboratory at Alexandria, Egypt. Lysimeters, 60 x 70 x 60 cm in size, were filled with a calcareous soil. Soil properties as determined according to Jackson (1960) were: $CaCO_3$ = 28.5%; clay content = 14.0%; silt, content = 23.8%; sand content = 33.4%; pH = 8.5, and EC_e= 0.78 dS/m.

The two tomato (*Lycopersicon esculentum*) varieties used were Edkawi, a comparatively salt tolerant land race widely planted in Egypt, and VF 145, a less salt-tolerant variey. A nursery, using the same calcareous soil, was prepared according to common grower practice. Four 28-day seedlings were transplanted into each lysimeter. The experimental design comprised four salinity treatments, two fertilizer regimes, and two varieties with four replications arranged in a complete randomized fashion. Salinity treatments were obatined by applying water of 0.52, 5.8, 8.5, and 11.0 dS/m conductivity. The first water was Alexandria tap water and the other three waters were obtained by adding NaCl and $CaCl_2$ (5:1 molar ratio) to the tap water. Salinity treatments started a week after transplanting. The first fertilization regime, an application of solid fertilizer (SF), was 20 kg N/A and 35 kg P_2O_5/A applied before transplanting, 30 kg N/A and 24 kg K_2O/A two weeks after transplanting, and 15 kg N/A and 12 kg K_2O/A at the flowering stage. The fertilizers were broadcast as ammonium nitrate, superphosphate, and potassium sulfate. The second fertilization regime, *i.e.* liquid fertilization (LF), was applications of the same total amount of the fertilizers used in SF-treatment, but split equally in the first of 12 irrigations after transplanting. Concentrated H_3PO_4, HNO_3, and K_2SO_4 were the sources for P, N, and K, respectively.

At the beginning of the flowering stage, developing and mature leaf samples were collected from each plant. For each leaf sample, fresh and dry weights were taken. Leaf dry matter was analyzed for Na content by flame photometry, Ca titrimetrically by the versenate method (Chapman and Pratt, 1961), and Cl by potentiometric titration on nitric-acetic acid extracts according to the procedure described by Cotlove (1963). Free proline in the leaves was extracted in sulfasalicyclic acid and determined colourimetrically with the acid-ninhydrine procedure as described by Bates et al. (1973). At harvest, fruit yield was determined, and total soluble salts (TSS) in the fruit determined by refractometry. Ascorbic acid was determined by direct titration of the filtered juice with 2,6-dichlorophenolindophenol dye as described in the AOAC Manual (1945).

RESULTS AND DISCUSSION

The general effect of salinity, method of fertilization, and variety on fruit yield, shoot dry weight, inorganic ions, and proline contents in developing and mature leaves as well as total soluble salts (TSS) and ascorbic acid in the fruits of tomato plants are summarized in Table 1.

Salinity, on average of the other variables, progresively and remarkably depressed growth as expressed by both the dry weight of shoots and fruit yields. At the highest salinity of 11 dS/m, growth and fruit yield were reduced to 38.1 and 33.0%, respectively, as compared to the growth and fruit yield results obtained under the control salinity (0.52 dS/m).

Similar results with tomato were obtained by Shalhevet and Yaron (1973) and Shannon et al. (1987). Salinity also resulted in considerable but variable increases in the Na, Ca, Cl, and proline contents in both developing and mature leaves. Under the control treatment (0.52 dS/m), the Na, Ca, and Cl contents in mature leaves were almost double that that had accumulated in the developing leaves. As salinity was increased to 11 dS/m, the Na, Ca, Cl, and proline contents were 209, 129, 103, and 3707%, respectively, of that under the control salinity in developing leaves. Respective increases in mature leaves were 897, 161, 2046 and 1065%. Sodium in particular, and Cl seemed to accumulate to a greater extent in mature leaves than in developing leaves. These results indicate that no dilution effect for inorganic ions had occurred in the leaves during plant growth. Proline, however, showed an opposite trend as it accumulated considerably in the developing leaves as compared to the mature leaves with increasing salinity. Shannon et al. (1987) reported similar results for the cultivated tomato "Heinz 1350".

With respect to total soluble salts and ascorbic acid contents in the fruits, salinity had very little effect on these parameters.

Solid and liquid fertilization brought different effects on plant growth, yield, and ion concentration in both developing and mature leaves (Table 1). Growth and fruit yield were greater with liquid fertilization (LF) than with solid fertilization (SF), the difference being 13.5% more yield. This could be attributed to the more efficiency of fertilizer availability and utilization with liquid application.

Over the range of salinity treatments and between the two tomato varieties, there was little increase in the Na, Ca, and Cl contents, and a small decrease in the proline content of both developing and mature leaves under the liquid fertilization method. Total soluble salts and ascorbic acid contents in tomato fruits were not materially affected.

On the range of the salinity and fertilization treatments, the two tomato varieties were very nearly the same in terms of growth and yield production. There

Table 1. The general effect of irrigation water salinity and fertilization method on growth, fruit yield and the accumulation of organic and in-organic solutes in the leaves of two tomato varieties.

Factor	Fruit yield g/plant	Shoots dry weight g/plant	Inorganic ions, mmol/kg dry wt. Na^+ Dv.L	Na^+ Mat.L	Ca^{++} Dv.L	Ca^{++} Mat.L	Cl^- Dv.L	Cl^- Mat.L	Proline umol/g fresh weight Dv.L	Proline Mat.L	TSS %	Ascorbic acid mg/100 g fr.juice
Salinity dS/m												
0.52	1146	258.6	32.2	64 .0	607.5	1130	100.8	175.0	19.6	24.3	5.21	22.54
5.80	773	159.1	46.3	165.5	795.0	1845	765.0	2377.0	63.0	42.0	5.55	23.48
8.50	550	114.4	52.8	317.5	880.0	2077	1135.0	3025.0	238.3	113.5	6.02	23.00
11.00	378	98.5	67.5	573.8	782.5	1822	1322.5	3582.5	726.5	258.8	6.21	22.53
LSD	19.2	4.83	1.15	5.8	18.1	31.3	19.1	43.4	4.3	2.3	0.36	0.58
Fertilization method												
S.F	667	145.6	48.5	276.4	735.0	1665	811.0	2217.5	273.5	111.9	5.69	22.5
L.F	757	169.7	50.9	284.0	797.5	1772.5	850.6	2362.5	250.2	107.4	5.81	23.22
LSD	13.6	3.4	0.96	4.1	12.8	22.1	13.5	30.7	3.1	1.6	n.s.	0.41
Variety												
Edkawi	715.4	156.5	56.5	285.9	816.3	1682.5	848.8	2305.0	219.6	99.0	6.00	23.20
VF 145	708.4	158.8	42.9	274.5	716.3	1755.0	812.9	2275.0	304.1	120.3	5.49	22.57
LSD	n.s.	n.s.	0.96	4.1	12.8	22.1	13.5	n.s.	3.1	1.6	0.26	0.41

n.s. denotes a statistically insignificant effect, at $P < 0.01$

were minor differences in the Na, Ca, and Cl contents of both developing and mature leaves between the two varieties. Proline, however, was higher in the VF 145 than in the Edkawi tomato variety, especially in the developing leaves.

Total soluble salts and ascorbic acid content in the fruits were a bit lower in the VF 145 than in the Edkawi tomato variety.

The interaction effects of salinity levels, method of fertilization, and tomato variety on the experimental parameters were computed and only those interactions that were of significance are given in Tables 2 and 3. No interaction effects between variety and fertilization method were found.

The two tomato varieties, though moderately salt-tolerant, proved to be affected differently by salinity regarding both yield and ion concentration in the leaves. The VF 145 tomato variety seemed a bit more sensitive to salinity than the Edkawi variety, taking both fruit yield and shoot dry weight in consideration (Table 2). Both the Na and Cl contents in either developing or mature leaves were noticeably higher in the Edkawi variety than in VF 145 vareity at lower salinitiies. But with increasing salinity, this difference became narrower. By contrast, Ca in mature leaves was equal in the two varieties under the control treatment (0.52 dS/m), but with increasing salinity, it became lesser in Edkawi than in VF 145 variety. Proline in either developing or mature leaves was a bit higher in Edkawi than in VF 145 variety at the lower salinity, but at higher salinity, the reverse occurred (Table 2).

Our results suggest that since both tomato varieties responded differently to salt stress, there is a differing physiological mechanism(s) involved in salt tolerance that probably exists in these two varieties. Similarly, Shannon et al. (1987) and Tal (1985) also concluded that the physiology of salt tolerance may differ among tomato varieties.

Liquid fertilization (LF) resulted in higher yields as compared to that obtained with solid fertilization (SF) at lower salinity levels. However, at higher salinity (*e.g.* 11.0 dS/m), the two methods of fertilization had the same effect on yield (Table 3). The same trend occurred with respect to Ca content in both developing and mature leaves. With respect to Cl content in mature leaves, at the control treatment (0.52 dS/m), solid and liquid fertilization had the same effect, but with increasing salinity, liquid fertilization (LF) resulted in more Cl accumulation in the leaves of plants than solid fertilization (SF). This suggests that mineral nutrition

Table 2. Salinity and variety interaction effects on yield and foliar contents of organic and in-organic solutes in tomato plants.

Variety	Salinity levels, dS/m.				
	0.52	5.80	8.50	11.00	LSD
	Fruit yield, g/plant				
Edkawi	1112	764	570	416	27.1
VF 145	1180	783	531	340	
	Shoot dry weight, g/plant				
Edkawi	250	157	119	100	6.8
VF 145	267	162	110	97	
	Na^+ in developing leaves, m mol/Kg dry weight				
Edkawi	39	55	62	71	1.6
VF 145	26	38	44	65	
	Na^+ in mature leaves, m mol/kg dry weight				
Edkawi	77	184	300	583	8.3
VF 145	51	147	335	565	
	Cl^- in developing leaves, m mol/kg dry weight				
Edkawi	130	800	1100	1380	27.0
VF 145	72	740	1180	1270	
	Cl^- in mature leaves, m mol/kg dry weight				
Edkawi	220	2450	2900	3650	61.4
VF 145	130	2300	3150	3510	
	Ca^{++} in mature leaves, m mol/kg dry weight				
Edkawi	1116	1810	1990	1780	44.3
VF 145	1110	1880	2170	1870	
	Proline in developing leaves, u mol/kg fresh weight				
Edkawi	23	58	203	594	6.1
VF 145	16	68	273	859	
	Proline in mature leaves, u mol/kg fresh weight				
Edkawi	29	44	106	216	3.2
VF 145	20	39	120	302	

Table 3: Salinity and method of fertilization interaction effect on yield and ions accumulation in tomato leaves.

Method of fertilization	Salinity levels, dS/m. 0.52	5.80	8.50	11.00	LSD
	Fruit yield, g/plant				
S.F	1059	718	526	365	27.1
L.F	1233	829	575	391	
	Shoot dry weight, g/plant				
S.F	235	145	107	96	6.8
L.F	282	173	122	101	
	Ca^{++} in developing leaves, m mol/kg dry weight				
S.F	560	755	855	770	25.6
L.F	660	835	905	795	
	Ca^{++} in mature leaves, m mol/kg dry weight				
S.F	1080	1790	2000	1800	44.3
L.F	1190	1910	2160	1850	
	Cl^{-} in mature leaves, m mol/kg dry weight				
S.F	160	2240	2930	3540	61.4
L.F	190	2510	3120	3620	
	Proline in developing leaves, umol/kg fresh weight				
S.F	20	68	251	756	4.3
L.F	20	59	226	697	
	Proline in mature leaves, umol/kg fresh weight				
S.F	25	44	116	263	3.2
L.F	24	40	112	255	

could possibly alleviate the depressive effect of salinity on yield up to a certain level (8.5 dS/m under the experimental conditions), but above which minreral nutrition is not likely to reduce the yield-depressing effect of salinity. Despite the fact that liquid fertilization enhanced plant growth and fruit yield, it also increased the concentration of inorganic ions in leaves. This might indicate that, under saline conditions, proper mineral nutrition results in a more efficient ion compartmentation that minimizes the depressive effect of salinity on cellular activity, and in turn, promotes plant growth and yield. In contrast to inorganic ions, free proline in both developing and mature leaves was equal under the two fertilization regimes, solid and liquid fertilization, at the lower salinity level (0.52 dS/m), but became greater under the solid fertilization treatment at the higher salinities.

CONCLUSIONS

Salt stress may impose metabolic, nutritional, and osmotic costs on nonhalophytes that in turn limit growth and development. Our study was an effort to examine the ameliorative effect of mineral nutrition on salt injury for two moderately salt-tolerant tomato varieties, *i.e.* VF 145 and Edkawi. The liquid fertilization regime used in this study is equivalent to a moderately high rate of broadcast N- and P-fertilization. However, the results obtained suggest that the ameliorative effect of mineral nutrition on plant growth and productivity is limited to low and moderate salinities. At high salinity levels, mineral nutrition amelioration becomes ineffective when tomato varieties responded similarly to each fertilization method.

Although both the VF 145 and Edkawi varieties were classed as moderately salt-tolerant; they responded differently to salinity level with regard to their accumulation of Na, Cl, Ca, and proline in developing and mature leaves. This suggests a difference in physiological response between the two varieties. The source for these differences needs further investigation.

In the non-saline control plants, proline accumulation, like the other inorganic ions, increased with plant age. In salt stressed plants, proline accumulation decreased with leaf age; however, more accumulation was attained by increasing salinity levels. This pattern of proline accumulation was similar in the leaves of both Edkawi (the more salt-tolerant) and VF 145 (the less salt-tolerant) tomato. However for the Edkawi variety, less proline accumulated in the leaves than that in the leaves of VF 145, which possibly suggests that proline accumulation is a result of salt stress rather than a cause of salinity resistance.

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