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Salt Tolerance in the Wild Relatives of the Cultivated Tomato: Responses of *Solanum pennellii* to High Salinity

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Summary. The cultivated tomato *Lycopersicon esculentum*, cultivar Rheinlands Ruhm, and the wild species *Solanum pennellii* accession Atico, were compared with respect to their salt tolerance. The wild species was found to be more salt tolerant than the cultivated tomato. In contrast to *L. esculentum* plants, the growth of the wild species was not impaired by the high salinity (Table 1), although the latter accumulated more Cl^- and Na^+ ions and its K^+ level decreased under salinity (Tables 3, 4, 5). The smaller increase in water deficit under salinity in the wild species, probably resulted from its higher accumulation of ions (Table 2).

Introduction

One way to exploit the large areas of saline soils and the abundant saline water sources of the world is the improvement of salt tolerance in the cultivated plant species. A most promising technique to achieve this goal may be the transfer of genes from closely related wild species adapted to high salinity.

In the genus *Lycopersicon* the two wild species *L. peruvianum* (Tal, 1971; Tal and Gavish, 1973) and *L. cheesmanii* (Rush and Epstein, 1976) were found to be more salt-tolerant than the cultivated species. Tal (1971) suggested that a better osmotic adjustment was responsible for the superior performance of the wild species *L. peruvianum* under salinity. The wild plants accumulated more Na^+ and Cl^- ions and their relative water content and total dry weight decreased less as compared with the cultivated tomato. Rush and Epstein (1976) found that the salt-tolerant ecotypes of *L. cheesmanii*, similar to *L. peruvianum*, accumulated more sodium and their growth was less impaired when grown in saline medium as compared with the cultivated tomato.

In the present paper the wild species *Solanum pennellii* and the cultivated tomato *L. esculentum* were compared with respect to their responses to salinity. These responses included: growth, water balance and accumulation of Na^+, K^+ and Cl^-. The wild species, which is genetically very close to the cultivated tomato (Rick, 1960; Tal, 1967), was found to be more salt-tolerant.

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Materials and Methods

(a) Plant Material and Growth Conditions

The species used in the present research were the cultivated tomato *Lycopersicon esculentum,* cv. Rheinlands Ruhm (Le), and the wild species *Solanum pennellii,* accession Atico, designated hereafter as Sp. The wild species was collected in a dry habitat in Peru (Rick, 1974).

Plants were grown in the greenhouse during the summer with day and night temperatures of about 30 and 20° C respectively. Seeds were sown in vermiculite and 10-day-old seedlings, having 1 – 2 leaves, were transferred one each to a plastic bottle containing 3 litres of aerated half-strength Hoagland solution (Hoagland and Arnon, 1950). The plants having about 4 leaves at the beginning of salt treatment. While control plants continued growing in the original solution, NaCl was added gradually (33 or 66 mol m^{-3} every 2 days) to plants of the treated groups to final concentrations of either 100 or 200 mol m^{-3}. Analyses represented in this paper were performed on 6-week-old plants bearing about 7 leaves, 14 days after the first addition of salt. Growth, relative water content, succulence and accumulation of Cl^- were also examined once in 9-week-old plants bearing flowers and the results were very similar to those obtained from the 6-week-old plants.

(b) Dry Weight

Shoots and roots of control and salt-treated plants were oven-dried at 85° C for 24 h and weighed.

(c) Relative Water Content and Succulence

Leaf discs 13 mm in diameter were punched from the center of the leaflets of the fourth leaf from the top. They were weighed (W_f) and floated for 4 hr on distilled water at 4° C, 20 cm below a 20 W fluorescent light and weighed again (W_s) (Slatyer, 1961). For dry wight (W_d) determination, the discs were oven-dried at 85° C for 24 h. Relative water content was calculated according to $[(W_f - W_d/(W_s - W_d)] \times 100$ and succulence according to W_f/W_d.

(d) Ion Concentration

Detached leaves (fourth from the top) and roots (rinsed for 3 minutes in 0.5 mol m^{-3}, $CaSO_4$ in water) were oven-dried at 85° C for 24 h, weighed and transferred to 3 cm^3 of 0.1 N nitric acid for 48 h at room temperature. Chloride was determined in samples of this solution with a Buchler-Cotlove chloridometer and sodium and potassium were determined with a Corning-Ell flame photometer.

Results

(a) Dry Weight of Shoots and Roots

The dry weight of both shoots and roots decreased only in the cultivated plants under salinity, the decrease of the shoot being, relatively, much greater (Table 1). The

Table 1. Dry weight of shoots and roots of control (0) and salt-treated (100 or 200 mol m^{-3}) Le and Sp plants. Each value is a mean of 10 plants (± standard error). The table represents the data of one out of five similar experiments

Species	Shoot/g			Root/mg		
	0	100	200	0	100	200
L. esculentum	2.67±0.34	2.10±0.10	1.02±0.15	286.1±36.0	243.6±19.9	190.9± 8.9
S. pennellii	0.29±0.06	0.23±0.02	0.22±0.03	45.8± 8.4	46.8±10.6	60.5±13.5

Table 2. Relative water content $(W_f - W_d)/(W_s - W_d)$ and succulence (W_f/W_d) of leaves of control and salt-treated Le and Sp plants. Each value is a mean of 5 plants. Other details as in Table 1

Species	Relative water content			Succulence		
	0	100	200	0	100	200
L. esculentum	81.17±2.17	71.59±2.25	66.37±1.10	7.43±0.23	8.04±0.28	8.65±0.53
S. pennellii	85.80±1.35	78.69±3.10	74.50±1.65	8.75±0.52	10.80±0.50	20.23±0.56

Table 3. Specific concentration of chloride in dry weight d_0 leaves and roots of control and salt-treated Le and Sp plants (c mol kg^{-1}). Each value is a mean of 5 plants. Other details as in Table 1

	Leaf			Root		
	0	100	200	0	100	200
L. esculentum	5.32±0.15	24.15±0.81	39.35±5.15	5.42±0.46	29.92±2.72	37.29± 4.97
S. pennellii	8.95±1.20	48.76±3.76	90.61±3.00	5.32±0.87	71.21±7.36	154.27±18.38

small changes in shoot and root growth in the wild species under salinity were statistically not significant. It can be concluded, therefore, that the growth of the wild plants was practically not affected by NaCl salinity, even as high as 200 mol m^{-3}.

(b) Relative Water Content and Succulence

Relative water content in the leaf decreased under salinity in both species, the decrease being somewhat greater in the cultivated species (Table 2). Leaf succulence increased very little in both species under salinity of 100 mol m^{-3} NaCl. Under the higher salinity, however, succulence increased very little in Le plants but considerably in the wild species.

(c) Ion Concentration

Chloride concentration per unit root and leaf dry weight increased in both cultivated and wild plants under salinity (Table 3). The increase was much greater in the root and leaf of the wild plants under both 100 and 200 mol m^{-3} NaCl.

Table 4. Specific concentration of sodium in dry weight d_0 leaves and roots of control (0) and salt-treated (100 or 200 mol m^{-3}) Le and Sp plants (c mol kg^{-1}). Each value represents the average of 5 plants (± standard error). The table represents the data of one out of two similar experiments

Species	Leaf			Root		
	0	100	200	0	100	200
L. esculentum	3.58±0.58	11.47±0.34	22.74±0.58	7.52±0.55	18.39±3.18	32.32±0.74
S. pennellii	8.97±0.56	26.76±2.34	50.02±7.58	6.29±1.44	37.26±3.28	63.46±5.38

Table 5. Specific concentration of potassium in dry weight d_0 leaves and roots of control and salt-treated Le and Sp plants (c mol kg^{-1}). Other details as in Table 4

Species	Leaf			Root		
	0	100	200	0	100	200
L. esculentum	61.21±9.12	63.97±6.30	81.33±8.70	55.42±5.57	36.16±3.99	52.87±10.01
S. pennellii	42.14±7.80	14.37±1.75	10.69±0.95	64.70±7.38	61.45±8.85	38.78± 8.07

As with chloride, sodium concentration was higher in the saline-treated plants (Table 4). The Sp plants accumulated more Na^+ than Le plants in both roots and leaves.

The concentration of K^+ did not decrease under salinity in the Le plants, except in the roots under 100 mol m^{-3} NaCl solution (Table 5). In the wild plants, however, K^+ concentration decreased under NaCl salinity in both roots and leaves.

Discussion

The wild species *Solanum pennellii*, which originated in an arid habitat in Peru, seems to be more tolerant to salinity than the cultivated tomato *Lycopersicon esculentum*. In contrast to the cultivated tomato, the growth of Sp, which accumulated more Cl^- and Na^+ ions, was not impaired by the high NaCl concentrations. Resulting probably from their higher accumulation of ions, the salinity induced increase of water deficit was smaller in the wild plants. It seems possible, in agreement with Bernstein's definition of salt tolerance (1963), that the Sp plants, like *L. peruvianum* (Tal, 1971) and probably also *L. cheesmanii* (Rush and Epstein, 1976), are more salt tolerant than Le plants because they can adjust their internal osmotic pressure with less sacrifice of growth. Tal, Heikin and Dehan (1978) grew calli prepared from the leaf, stem and root of the cultivated tomato and *L. peruvianum* and *S. pennellii* plants on media containing various concentrations of NaCl. They found that the calli behaved in a similar fashion to the whole plants under salinity, i.e. the growth of calli derived from the wild species was less impaired under salinity as compared with those derived from the cultivated species, and they accumulated more Cl^- and Na^+ and less K^+ than the latter. They suggested, therefore, that the better osmotic adjustment, which characterizes the wild plants under high salinity, is operating at the cellular level and does not depend on the organization of these cells in the whole plant.

Unlike plant of *L. peruvianum* (Tal, 1971) and *L. cheesmanii* (Rush and Epstein, 1976) the growth of Sp plants was not decreased by a high salt concentration. Tal (1971) found that total plant dry weight decreased by 50% in young *L. peruvianum* plants growing in a solution containing 196 mol m^{-3} NaCl. Rush and Epstein (1976) found that although there were obvious differences in the appearance of plants of the wild species *L. cheesmanii* and the cultivated tomato, both species exhibited reduced growth rates even under mild salt conditions.

Similar to *L. peruvianum* and *L. cheesmanii* plants and in contrast to the cultivated tomato, Sp leaves did not selectively absorb K^+ over Na^+ under high salinity inesmuch as K^+ level dropped while Na^+ concentration increased in the tissue. In the roots, however, the K^+/Na^+ ratio decreased more in the cultivated plants under salinity.

The Sp plants which are more salt-tolerant than the cultivated tomato, also seem to be more drought resistant. Yu (1972) found that leaves of Sp plants have higher ability than the cultivated ones to absorb water vapours from the surrounding atmosphere. He also found that this ability was inherited in plants of hybrid generations between the two species.

Unlike *L. peruvianum* (Rick and Butler, 1956) and similar to *L. cheesmanii,* the cross between Sp and the cultivated tomato is performed very easily and the hybrids are vigorous and fertile (Rick, 1960; Tal, 1967). Consequently, Sp plants may be used as a source of genes to increase the salt tolerance and probably also drought resistance of the cultivated tomato.

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