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Comparative Studies on the Sodium, Potassium, and Chloride Relations of a Wild Halophytic and a Domestic Salt-Sensitive Tomato Species[1]

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ABSTRACT

In long-term experiments with differentially salinized nutrient solutions, plants of *Lycopersicon esculentum* Mill cv. Walter failed at Na^+ concentrations of 200 millimolar or more but tolerated K^+ concentrations of that magnitude. The behavior of the wild, salt-tolerant *Lycopersicon cheesmanii* (Hook) C. H. Mull., accession number 1401, was diametrically different; it tolerated Na^+ at 200 millimolar, but K^+ at the same concentration proved toxic to it.

Short-term comparative studies on the absorption and translocation of Na^+, K^+, and Cl^- of the two species were carried out using radioactive tracers with excised roots and whole plants. These studies showed that, under high salt conditions (50–100 millimolar NaCl), the tolerant 1401 freely accumulated Na^+ in the shoot, while the salt-sensitive cultivar excluded it from the leaves, where it has been shown to be toxic.

In experiments where K^+ was limiting, the salt-tolerant species could partially substitute Na^+ for K^+. Sodium stimulated growth even when K^+ was present at adequate concentrations. The domestic cultivar could not substitute Na^+ for K^+ and showed no similar growth stimulation when Na^+ was added in the presence of adequate K^+. The salt-tolerant 1401 was more efficient in K^+ absorption than was the domestic cultivar at both low and moderate ambient K^+ concentrations.

The two species differed little in their chloride relations.

The roles of K^+ and Na^+ in plant nutrition have sparked numerous investigations which ultimately have led to the conclusion that K^+ is the only monovalent cation that is essential for all higher plants (7) but that Na^+ can have beneficial effects on plant growth. Sodium has been shown to be essential for a few species (4) and for improvement in growth and productivity in several crops, particularly those in the family Chenopodeaceae (11, 15, 23). There is substantial evidence that plants of moderate to high salt tolerance may, under saline conditions, accumulate large amounts of salt and that Na^+, in particular, can make a significant contribution to both the osmotic relations (5, 8, 13, 21) and the mineral nutrition of those plants, especially if K^+ is present at less than optimal concentrations (3, 15).

Several of the studies on Na^+ and K^+ relations of crop plants have included the tomato. Some wild species and domestic cultivars have been shown to be 'salt excluders' (9, 22) and some 'salt accumulators' (16, 18, 19), while still others have been considered intermediate in their response to salinity (2, 5, 14).

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In experiments reported here, we compare a wild salt-tolerant ecotype of *Lycopersicon cheesmanii* with a glycophytic domestic *L. esculentum* cultivar in terms of their absorption and translocation of Na^+, K^+, and Cl^- and of their growth responses to these ions, especially the cations.

MATERIALS AND METHODS

Comparative Rates of Potassium Absorption: Excised Roots. Potassium absorption experiments using the 'tea bag' technique (6) were done with roots excised from 30- to 40-day-old plants of two species of tomato. Seeds of *L. esculentum* Mill. cv. Walter, a salt-sensitive variety, and *L. cheesmanii* ssp. minor (Hook) C. H. Mull., accession 1401, a wild, salt-tolerant ecotype from the Galapagos Islands of Ecuador (17, 18), were germinated in the dark, on cheesecloth-covered stainless steel screens placed on 3.5-L plastic containers of half-concentration modified Hoagland solution (7). See Rush and Epstein (18) for a detailed description of the *L. cheesemanii* seed preparation. The *L. cheesmanii* ecotype is slower in germination and seedling establishment than is Walter and was planted 10 days prior to Walter to provide seedlings of similar size and physiological development. Similar-sized plants of both species were used in all experiments.

Triplicate 1-g samples of roots of the two species were exposed to $^{86}Rb^+$-labeled KCl solutions which ranged in concentration from 0.01 to 50 mM. Several experiments done with $^{86}Rb^+$ and $^{42}K^+$ showed Rb^+ to be an acceptable analog for K^+ in tracer studies in the tomato. Root samples were placed in aerated containers of the $^{86}Rb^+$-labeled KCl solutions to which $CaSO_4$ had been added to a concentration of 0.5 mM. Exposure time for all experiments was 30 min. The samples were then rinsed in ice-cold 0.5 mM $CaSO_4$ for 15 min and counted by liquid scintillation. The absorption of K^+ was measured by reference to the 'specific activity' of the $^{86}Rb^+$-labeled K^+ of the experimental solutions.

Absorption and Translocation of Sodium, Potassium, and Chloride: Entire Plants. Seedlings about 5 cm tall were placed in the central holes of 5-cm diameter, Parafilm (American Can Company Dixie/Marathon, Greenwich, CT)-covered cork stoppers. Roots were threaded through a 3-mm hole punched in the film, and the hypocotyl was wrapped with Dacron batting for support. The seedlings were planted in 12-L containers of 0.1 concentration modified Hoagland solution. The covered cork stoppers provided floatable hydrophobic platforms that could be placed on the surface of labeled absorption solutions. This method prevented root damage before and during the experiments, which were designed to measure short-term ion absorption and translocation in undamaged whole plants.

Roots of intact seedlings 14 to 17 cm in height were placed in gently aerated 50 mM solutions of $^{86}Rb^+$-labeled KCl, $^{22}Na^+$-labeled NaCl, or $^{36}Cl^-$-labeled KCl, each containing 0.5 mM

$CaSO_4$. Care was taken to have no part of the plant other than the roots in contact with the experimental solutions. The plants were removed from the labeled solutions at the end of 30 min and immediately separated into roots, stems, petioles, and leaves. The roots were placed in an aerated ice-cold 0.5 mM $CaSO_4$ desorption solution for 15 min. Fresh weights were taken and the tissues processed and counted by liquid scintillation. The plants were grown and the experiments carried out in a controlled environment chamber with a day length of 14 h and day and night temperatures of 20 ± 2 and 30 ± 2°C, respectively.

Autoradiography. Roots of seedlings of both species, 14 to 18 cm in height, were placed in solutions of $^{86}Rb^+$-labeled KCl or $^{22}Na^+$-labeled NaCl at concentrations of 0.5 mM or 100 mM for 1 h; the solutions also contained 0.5 mM $CaSO_4$. There followed a 15-min desorption period in ice-cold aerated 0.5 mM $CaSO_4$. The whole plants were then quick-frozen with Dry Ice and placed in a freeze-dryer for 21 days. Immediately upon removal they were mounted, placed on X-ray film, and stored in shielded containers. Exposure time was 40 to 45 days. Plants were grown and experiments carried out in a controlled environment chamber.

Sodium Substitution. Throughout these experiments, care was taken to avoid contamination by Na^+ or K^+ as much as possible. Small seedlings (3–5 cm in height) were transplanted to 12-L containers, four plants per container. Four treatments were used: complete nutrient solution; nutrient solution in which all of the K^+ was deleted; nutrient solution in which all of the K^+ was replaced by Na^+; and nutrient solution in which one-half of the K^+ was replaced by Na^+. Undiluted nutrient solution contains about 6 mM K^+. Duration of the experiments was 20 to 25 days from transplanting. The plants were observed and photographed, and fresh and dry weights were taken to evaluate the extent to which Na^+ could substitute for K^+ in both species.

In another set of experiments aimed at evaluating the role of Na^+ as a nutrient, seedlings 6 to 8 cm in height were planted in the lids of 3.5-L containers of nutrient solution to which no K^+ had been added, using the cork stopper method. There was one plant per container. The NO_3^- salts of K^+ and Na^+ were added singly or in combination for a total of 10 mmol/plant. The undiluted nutrient solution contains about 21 mmol K^+ in 3.5 L. The nitrogen was adjusted to the concentration of the undiluted nutrient solution by the addition of NH_4NO_3. Sodium and K^+ were added at the following concentrations (K^+/Na^+ in mmol/plant): 10/0, 9/1, 7/3, 5/5, 3/7, 1/9, and 0/10. The mineral salts were not replenished during the experiment. Each treatment was done in triplicate. The experiments were terminated when the *L. esculentum* plants in the 10/0 treatments showed moderate K^+ deficiency symptoms. This occurred 24 to 28 days after transplanting. Fresh and dry weights were taken and averaged for each treatment and for each species. Nutrient solutions were analyzed for Na^+ and K^+ at the beginning and end of each experiment. In a replication of the experiment, nutrient solutions were sampled daily and depletion curves plotted for Na^+ and K^+ for all treatments. Experiments were carried out in the greenhouse under conditions of ambient light during spring and early summer.

Potassium and Sodium Toxicity. Seedlings, 6 to 8 cm in height, were transplanted into the lids of 42-L tanks of aerated, undiluted nutrient solution using the cork stopper method. Each tank contained six plants; there were two tanks per treatment. Potassium chloride or NaCl was added at a rate of 50 mM at 5- to 7-day intervals, starting 7 days after transplanting. Salts were added until the concentration was about 250 mM KCl or NaCl. The control treatments had no additional salts added except for pH adjustment. Visual observations and comparisons were made along with photographs to evaluate plant responses.

The experiments were repeated as described above, except that the counterions of the K^+ and Na^+ were equivalent parts of Cl^-, SO_4^{2-}, and NO_3^-, thus eliminating the dominance of a single anion. Experiments were carried out in the greenhouse at ambient light in the winter and spring.

RESULTS

Excised Root Experiments. Over the range of K^+ concentrations up to 0.2 mM (7), rates of absorption did not exceed 4.4% and 2.7% of the highest rates attained at a concentration of 50 mM by *L. cheesmanii* and *L. esculentum*, respectively (Fig. 1). At all concentrations, especially the lowest (0.01–0.10 mM), the salt-tolerant *L. cheesmanii* ecotype absorbed much more K^+ than did the *L. esculentum* cultivar. At 0.01 mM K^+, the rate of absorption by roots of *L. cheesmanii* exceeded that of *L. esculentum* by a factor of 14.7. That factor narrowed at the higher concentrations but was still 1.59 at 50 mM K^+.

Absorption and Translocation of Na^+, K^+, and Cl^- in Whole Plants. The *L. cheesmanii* 1401 absorbed and translocated larger amounts of Na^+ and Cl^- than did the domestic *esculentum* cultivar (Table I). Only the roots of *L. cheesmanii* contained less Na^+ than those of *L. esculentum*, by almost a factor of two. Sodium absorption and distribution in the two species differed markedly. The salt-tolerant *L. cheesmanii* 1401 rapidly distributed Na^+ throughout the plant. The highest concentrations were in the shoot, with fairly even distribution in the stem, petioles, and leaves. The *L. esculentum* cultivar absorbed significantly less Na^+ and retained the highest concentration in the roots. Distribution of K^+ in the roots, stems, petioles, and leaves was similar in both species. Most of the K^+ was held in the roots. Progressively lower concentrations were found in the stems, petioles, and leaf blades, respectively.

Chloride was absorbed and translocated at a lower rate than either Na^+ or K^+ in both species. The distribution pattern was similar to that of Na^+ in that more Cl^- was exported to the upper plant in the *L. cheesmanii* ecotype while, in the domestic cultivar, the relative concentrations were highest in the roots and lowest in the leaves (Table I).

Autoradiography. Visual evaluation of the K^+ autoradiographs (not shown) was consistent with the findings from the short-term whole-plant experiments. The pattern of K^+ distribution was similar in both species (Table I).

The findings on Na^+ distribution were different, as expected from the data of Table I. At the low Na^+ levels (0.5 mM NaCl), there was a visible difference between the two species in the quantity of Na^+ absorbed, but the distribution was similar (Fig. 2). Most of the Na^+ remained in the roots and stems in both species. At the high concentration (100 mM NaCl), the entire plant outline of the salt tolerant *L. cheesmanii* ecotype is clear, showing rapid and fairly uniform distribution of Na^+. The distribution pattern of Na^+ in the sensitive *L. esculentum* cultivar was similar at both concentrations, but the exposure was more intense at the

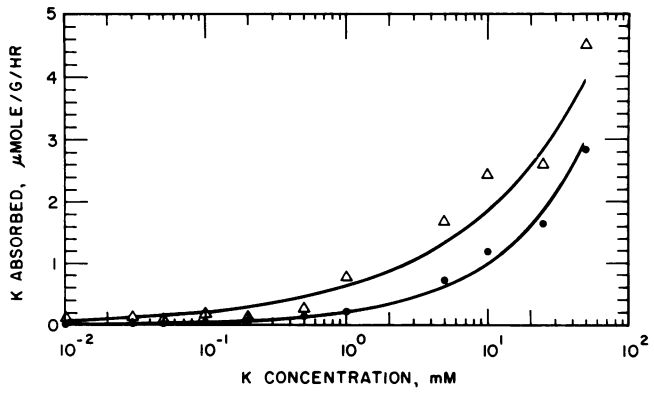

FIG. 1. Rates of K^+ absorption by excised roots of two tomato species as a function of the external K^+ concentration over the range 0.01 to 50 mM. (△), *L. cheesmanii*; (●), *L. esculentum*.

Table I. *Absorption and Distribution of Na^+, K^+, and Cl^- in Salt-Tolerant L. cheesmanii and Salt-Sensitive L. esculentum*

The data are given in μmol of ion/g fresh weight of tissue·h. Absorption time was 0.5 h, and solution concentrations were 50 mM Na^+, K^+, or Cl^- in 0.5 mM $CaSO_4$.

	L. cheesmanii						*L. esculentum*					
	Na^+		K^+		Cl^-		Na^+		K^+		Cl^-	
	μmol/g	SE	μmol/g	SE	μmol/g	SE	μmol/g	SE	μmol/g	SE	μmol/g	SE
Roots	5.20	0.05	11.08	0.37	5.68	0.18	9.99	0.30	13.77	0.44	5.90	0.14
Stems	9.17	0.13	5.95	0.20	5.50	0.15	1.79	0.08	4.10	0.16	2.13	0.07
Petioles	11.57	0.12	3.85	0.26	4.84	0.32	1.46	0.21	3.27	0.15	2.91	0.07
Leaves	8.10	0.21	1.32	0.03	3.49	0.18	1.10	0.10	2.31	0.17	1.75	0.03
Total	34.04		22.20		19.51		14.34		23.45		12.69	

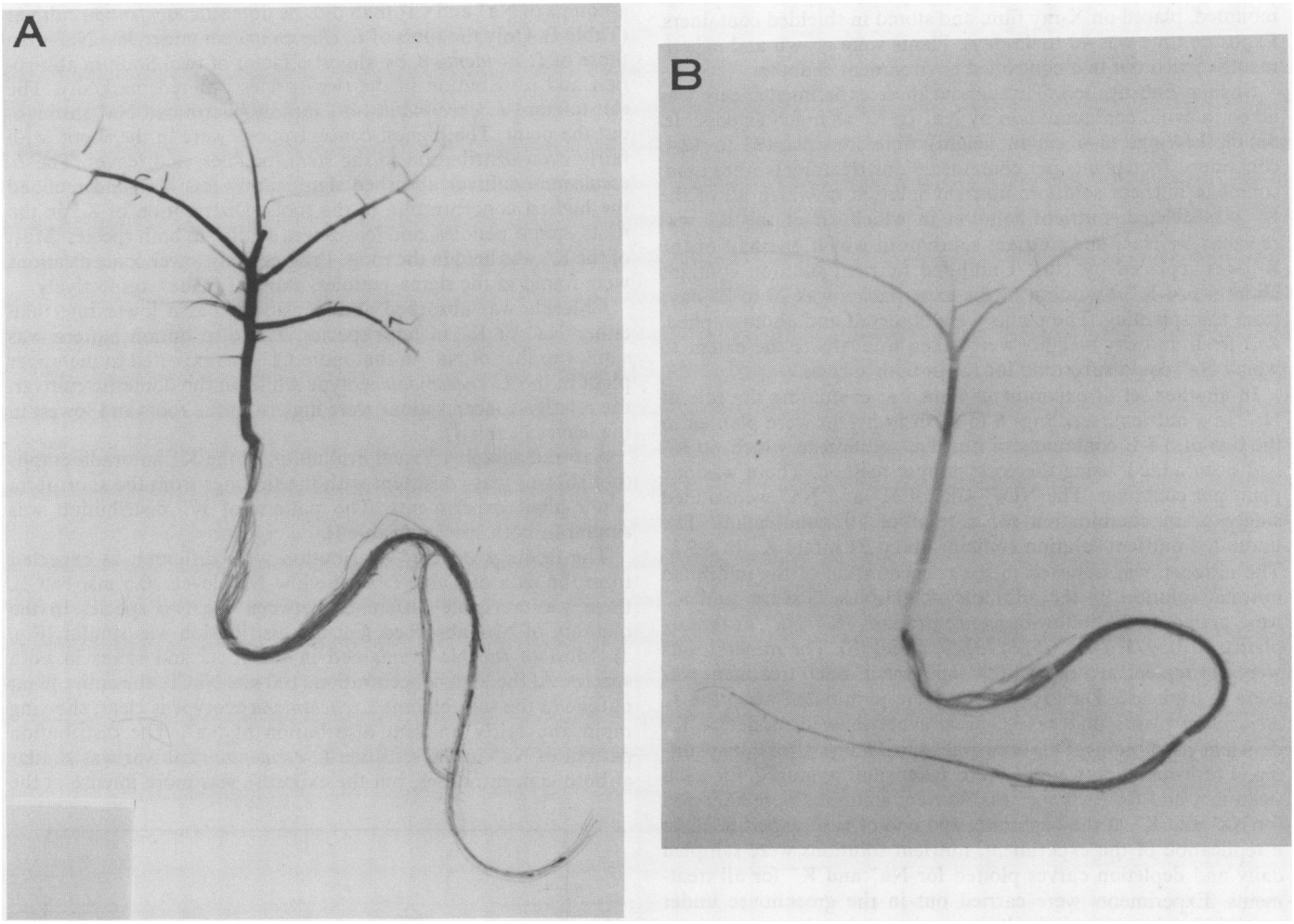

FIG. 2. A, Taken from an autoradiograph of the salt-tolerant *L. cheesmanii* ecotype exposed to 0.5 mM NaCl labeled with $^{22}Na^+$. B, Salt-sensitive *L. esculentum* cultivar showing that much less Na^+ has been absorbed. Note that, while concentrations are different, distribution is similar in both species at this low concentration.

high (100 mM) concentration, indicating greater absorption. A substantial quantity of Na^+ was absorbed into the roots and stem, but very little moved into the leaves (Fig. 3).

Sodium Substitution. The responses of the two species to substitution of Na^+ for K^+ differed markedly. Sodium was partially able to substitute for K^+ in the tolerant *L. cheesmanii* ecotype but not in the *L. esculentum* variety. The extent of Na^+ substitution was evaluated by visual comparison (Fig. 4) and dry weight yield (Table II). Sodium slightly improved growth of the salt-tolerant 1401 when compared with the treatment with neither Na^+ nor K^+, but it could not substitute completely for K^+ (Fig. 4). The treatment containing equal parts of Na^+ and K^+ resulted in larger plants than did the K^+-only control in this species.

The effect of various ratios of Na^+ and K^+ on dry weight was measured for both species (Table II). Ratios varied from 10/0 to 0/10 (mmol/plant) K^+/Na^+. The salt-tolerant *L. cheesmanii* increased relative dry matter production when Na^+ was present in addition to K^+ and produced 120% of the K^+-only control dry matter when the K^+/Na^+ ratio was 9/1. The dry matter production when the K^+/Na^+ ratio was 7/3, 5/5, or 3/7 was nearly equal to

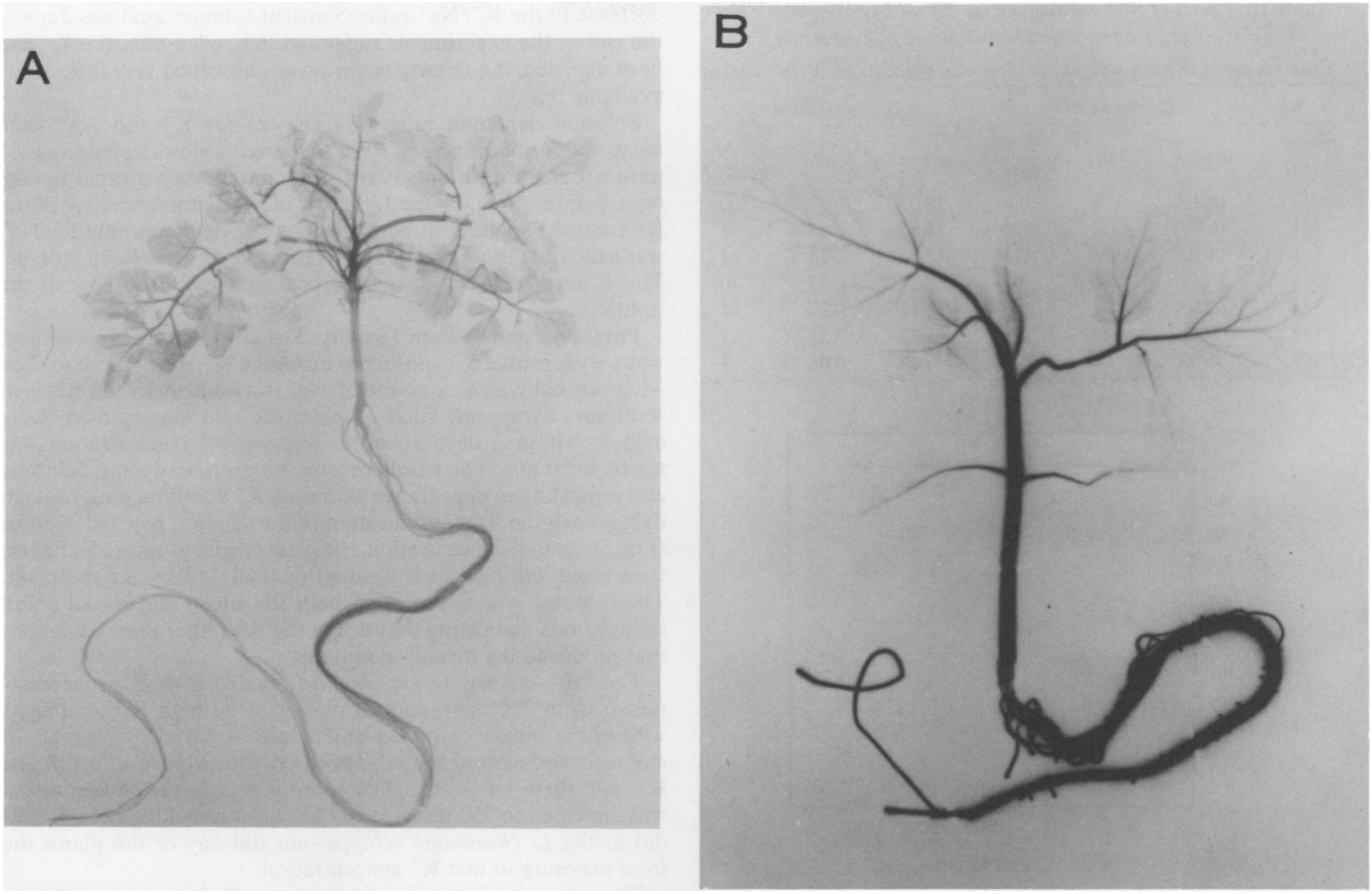

FIG. 3. A, Autoradiograph of the tolerant *L. cheesmanii* ecotype, showing that Na^+ distribution is rapid (exposure to the $^{22}Na^+$-labeled 100 mM NaCl solution lasted 1 h) and uniform throughout the plant when it is exposed to a high salt concentration. B, Salt-sensitive *L. esculentum* cultivar under the same salt conditions. Note that, while considerable Na^+ is absorbed, little is allowed into the leaves, where it has been shown to be toxic to this species.

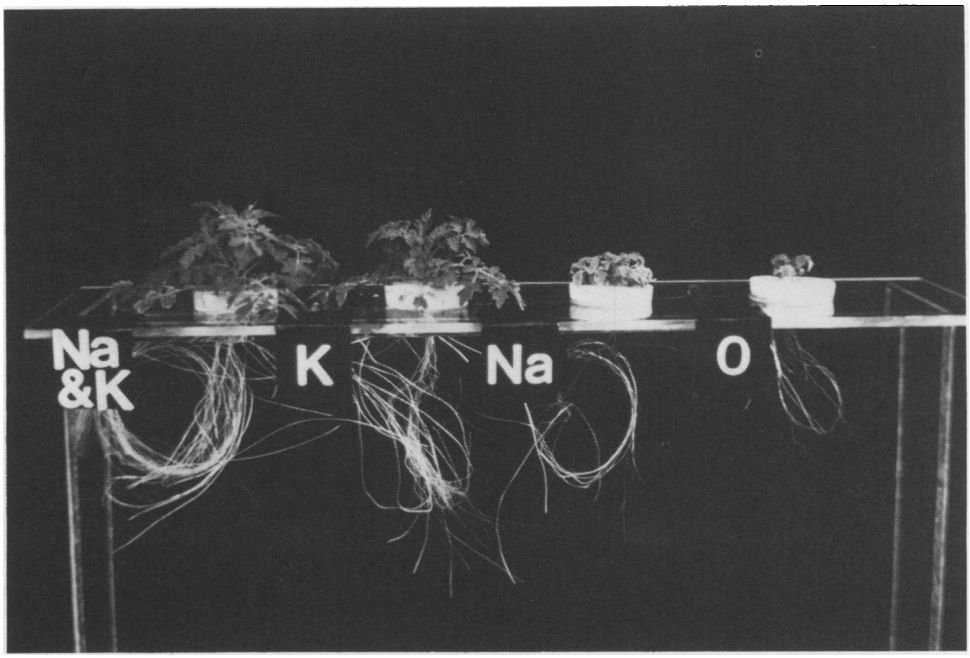

FIG. 4. Plants of the salt-tolerant *L. cheesmanii* were compared after being grown in nutrient solutions containing (left to right): equal parts Na^+ and K^+; K^+ but no Na^+; Na^+ but no K^+; neither Na^+ nor K^+. The largest plant is 10 cm tall.

or greater than that of the K^+-only control. Most of the Na^+ added to the *L. cheesmanii* ecotype was removed from the nutrient solutions, except in the 0/10 treatment. This indicated that Na^+ was being absorbed, and the increase in dry weight production

Table II. *Effects of Na^+ Substitution for K^+ on Dry Weight of Salt-Tolerant L. cheesmanii and Salt-Sensitive L. esculentum*

Data are given in g dry weight per plant and percentage of 10/0 control.

K/Na	*L. cheesmanii*			*L. esculentum*		
mmol/plant	*dry wt*	*SE*	*% of control*	*dry wt*	*SE*	*% of control*
10/0	14.15	0.79	100	19.05	0.50	100
9/1	16.96	0.53	120	16.85	0.65	88
7/3	15.70	0.55	111	15.84	0.24	83
5/5	13.45	0.60	95	13.39	0.33	70
3/7	13.60	0.38	96	12.14	0.27	64
1/9	9.72	0.48	69	6.22	0.31	33
0/10	0.70	0.04	5	0.49	0.05	3

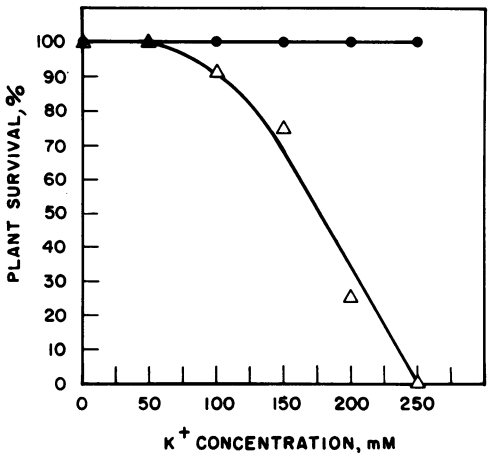

FIG. 5. Survival of *L. esculentum* and *L. cheesmanii* at increasing ambient K^+ concentrations. The K^+ was added in 50 mM increments as a mixed anion salt (Cl^-, SO_4^{2-}, and NO_3^-). (△), *L. cheesmanii*; (●), *L. esculentum*.

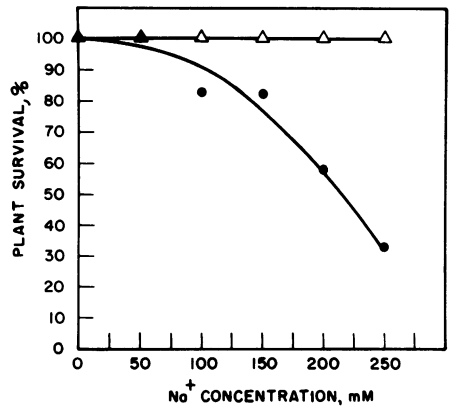

FIG. 6. Survival of *L. esculentum* and *L. cheesmanii* at increasing ambient Na^+ concentrations. The Na^+ was added in 50 mM increments as a mixed anion salt (Cl^-, SO_4^{2-}, and NO_3^-). (△), *L. cheesmanii*; (●), *L. esculentum*.

over the K^+-only control suggested that Na^+ could partially substitute for K^+ in this species. The 0/10 treatment produced only 5% of the 10/0 control dry matter, showing that at least some K^+ is necessary for the tolerant ecotype. *L. cheesmanii* does not, however, appear to be as efficient as the domestic cultivar in dry matter production per unit of K^+, but this could be the result of its slower growth rate (Table II).

The salt sensitive cultivar showed little ability to substitute Na^+ for K^+. Dry weight decreased almost linearly ($r = 0.94$) with the decrease in the K^+/Na^+ ratio. Nutrient solution analyses done at the end of the experiments suggested that, even after the K^+ had been depleted, the *L. esculentum* variety absorbed very little of the available Na^+.

Solution depletion rates (not shown) for K^+ and Na^+ were measured for both species. Results showed a slow depletion of K^+ until about the 14th day after transplanting; then a rapid uptake occurred, resulting, by the 18th day, in nearly total removal of the K^+ from the solution in both species. The depletion rate for Na^+ was nearly identical with that of K^+ for the *L. cheesmanii* ecotype. The *L. esculentum* cultivar absorbed little Na^+ from any of the solutions.

Potassium and Sodium Toxicity. The salt-tolerant *L. cheesmanii* was very sensitive to exposure to excessive K^+, much more so than when an equivalent amount of Na^+ was added to the nutrient solutions. Symptoms such as chlorosis and slow growth were evident within 3 days after the solution K^+ concentration was raised to 50 mM. The plants became progressively more chlorotic and unhealthy in appearance with each K^+ addition, most of them dying when the K^+ concentration of the solution reached 200 mM (Fig. 5). At that concentration, the plants suffered severe leaf burn, then rapid wilting which resulted in total collapse of the plant. The response was the same in both the single and mixed anion salinizations, indicating that it was the K^+ rather than the anions that produced the toxicity symptoms.

The salt-sensitive *L. esculentum* tolerated high K^+ concentrations (up to 250 mM), and all plants in the high K^+ treatments with either single or mixed anion salts survived. Symptoms of chlorosis and slowed growth appeared with exposure to 150 mM K^+, and these became slightly more severe as the concentration was increased to 250 mM K^+. No leaf burn or wilting occurred, as did in the *L. cheesmanii* ecotype, nor did any of the plants die from exposure to that K^+ concentration.

The response of the tolerant ecotype to Na^+ was quite different from that to K^+. Sodium was much less toxic than K^+ at equivalent exposure concentrations (Fig. 6). All the plants survived when exposed to 250 mM Na^+, and toxicity symptoms (reduced growth and slight chlorosis) were not as severe as when the plants were exposed to K^+. The tolerance of this species to Na^+ salts has been described elsewhere (18); the effects of excessive Na^+ in the present investigation were similar to those results.

Response to Na^+ in the salt-sensitive species was quite different from that to K^+. Chlorosis and reduced growth first appeared after exposure to 100 mM Na^+ and became progressively worse as the Na^+ level was increased. The plants showed symptoms of severe wilting at 200 mM Na^+. Only about 33% of those exposed to 250 mM Na^+ survived in either single or mixed anion salt solutions, suggesting that Na^+, rather than the anion, was the toxic agent.

DISCUSSION

There is considerable evidence that salt exclusion (specifically Na^+ exclusion) is the mechanism of survival for most species of agricultural importance when they are exposed to saline conditions (8, 10). Besford (2, 3) and Fong (9) have shown such trends in several tomato varieties and have concluded that there are 'Na^+ excluders' and that, when Na^+ is absorbed and translocated to the shoot, 'it was found that most of the Na^+ transported to the leaves was excluded from the laminar tissue and accumulated in the adjacent petioles' (3). Such studies have also shown that these salt-excluding tomatoes were not particularly salt-tolerant. The data from our experiments with Walter complement the findings on other tomato varieties. This exclusion mechanism contrasts with the response of most halophytes, which tend to accumulate salts as a mechanism for osmotic adjustment and nutritional supplementation when exposed to even moderate salinity (4, 8, 12).

The difference between salt absorption and toleration and salt

exclusion can be used as a measure of the degree of halophytism. The wild *L. cheesmanii* studied in the work reported here has been shown to be quite salt-tolerant (18, 19). Its responses to salt correspond to those of typical halophytes. The *L. esculentum* variety, Walter, shows no such tolerance of Na^+ and tends to exclude it from the leaves, where it is toxic. The absorption of Na^+ could be a key for use in the evaluation of germplasm in a selection and breeding program aimed at improving the salt tolerance of the tomato (19) and, probably, other crops.

There is evidence that Na^+ may be actively sequestered in the xylem parenchyma of several excluder species (7). This is a reasonable explanation of why Na^+ concentrations remain low in the leaf laminae of the sensitive tomato variety even when Na^+ is present in other parts of the plant. Sodium does not appear to be similarly toxic to *L. cheesmanii* and is not excluded from its leaf tissue. In fact, the evidence presented here and by others (5, 15) strongly suggests that Na^+ can, in some cases, partially substitute for K^+ and can even stimulate growth when supplied in addition to adequate K^+. Possible mechanisms include function as a 'cheap osmoticum' (24) or as a micronutrient involved in enzyme activation or other roles (4, 14). Increases in fresh and dry weight production elicited by the addition of Na^+ and tolerance of high tissue Na^+ concentrations in *L. cheesmanii* suggest that one or more of the above mechanisms are operating.

Another prominent difference between the two species studied is the response to high external K^+ and Na^+ concentrations. The salt-sensitive *L. esculentum* tolerates high K^+ concentrations, which are toxic to *L. cheesmanii*, in a manner similar to the way that the *L. cheesmanii* ecotype tolerates Na^+, which is toxic to *L. esculentum*. Ashby and Beadle (1), Stelzer and Läuchli (20), Storey and Wyn Jones (21), and Yeo *et al.* (25) found K^+ to be similarly toxic in other halophytic species.

From evidence presented here and from earlier studies (18, 19) involving *L. cheesmanii* and several domestic tomato varieties, three main conclusions emerge: (a) *L. cheesmanii* responds to salt stress in much the same way that many other halophytes do; (b) effects of specific ions can dominate the responses of plants to salinity, and even closely related genotypes can diametrically differ in this regard; and (c) leaf Na^+ content is positively correlated with salt tolerance and might be used as an index of salt tolerance in tomatoes.

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