Aust. J. Plant Physiol., 1983, **10**, 109–17

Salt Tolerance in the Wild Relatives of the Cultivated Tomato: Responses of *Lycopersicon esculentum*, *L. cheesmanii*, *L. peruvianum*, *Solanum pennellii* and F_1 hybrids to High Salinity

M. Tal[A] *and M. C. Shannon*[B]

[A] Department of Biology,
Ben Gurion University of the Negev,
Beer Sheva, Israel.

[B] U.S. Salinity Laboratory,
4500 Glenwood Drive,
Riverside, California 925001,
U.S.A.

Abstract

The performance of three wild relatives of the cultivated tomato (*Lycopersicon cheesmanii*, *L. peruvianum* and *Solanum pennellii*) and two tomato cultivars in control and saline media was compared. The parameters studied were elongation rate of the main stem, succulence, and accumulation of Na^+, K^+, and Cl^- in the roots, stem, leaf, and shoot tip. The same parameters but in the leaf only were also studied comparatively in two of the wild species *L. cheesmanii* and *S. pennellii*, the same two cultivars, and F_1 hybrids.

Under control conditions, the elongation rate of the stem of the two cultivars was higher than that of the wild plants, but under salinity it was relatively lower. Among all species, *S. pennellii* was the most succulent in all its major parts under both control and saline conditions. The wild species, especially *S. pennellii*, showed high accumulation of Na^+ in the leaf and top and a greater decrease in K^+ content under salinity as compared with the cultivated plants. In all three species, Na^+ probably substitutes for potassium in, at least, some of its physiological functions.

Complete dominance of *S. pennellii* over the cultivated plants is indicated for the relative decrease of elongation rate and K^+ level and for the increase of succulence under salinity. In contrast, *L. cheesmanii* seems to be completely dominant only for the relative decrease of K^+ under salinity.

Introduction

One approach to the exploitation of saline soils is the improvement of the salt tolerance of cultivated species. This may be achieved by exploiting intraspecific variability (Dewy 1962; Greenway 1962; Epstein *et al.* 1979) or, in species lacking such variability, genes may be transferred from closely related wild species adapted to high salinity.

Wild relatives of the cultivated tomato can be used as a source of genes for high salt tolerance. Tal (1971) and Dehan and Tal (1978) found that plants of *Lycopersicon peruvianum* and *Solanum pennellii* suffered under salinity less than the cultivated tomato. Compared with the cultivated tomato, these wild species showed a lower decrease in dry weight and relative water content under salinity, and they were more succulent and accumulated more Na^+ and Cl^- and less K^+. Rush and Epstein (1976, 1981) reported similar results for *L. cheesmanii* grown in sea water.

0310-7841/83/010109$02.00

In the present work, intact plants of the three wild species *L. cheesmanii*, *L. peruvianum* and *Solanum pennellii*, two tomato cultivars and F_1 hybrids were compared with respect to their response to high salinity. Such comparative studies of different species will facilitate the evaluation of their relative performance and the characterization of the mechanisms which contribute to their salt tolerance. Such a study may also reveal the dominance relationships between the wild species, on the one hand, and the cultivated species, on the other hand, for these characteristics, a knowledge which is essential for effective breeding for salt tolerance.

Materials and Methods

Plant Material

The species used in the present research included the cultivated tomato *Lycopersicon esculentum* Mill. cvv. Heinz 1350 (H) and VF 234 (VF), the wild species *L. cheesmanii* Riley ecotype No. 1400 (Lc), *L. peruvianum* (L.) Mill. (Lp), and *Solanum pennellii* Cor. accession Atico (Sp), and the F_1 hybrids between each of the cultivars and each of the two wild species Lc and Sp, the cultivars being used as the maternal parents. Seeds of the wild species were collected by Dr C. M. Rick of the University of California, Davis, from plants growing in dry habitats: Lc in the Galapagos Islands, Lp in Chile and Sp in Peru.

Plants were grown in the greenhouse during the winter with day/night temperatures of about 20/10°C. Seeds of H, VF and Lp and the F_1 hybrids were sown in vermiculite. Seeds of Lc and Sp were sown on wet filter paper in petri dishes after treatment with a solution of hypochlorite (3·5% active chlorine), those of Lc for 90 min and those of Sp for 45 min. The hypochlorite dissolves the seed coat, which prevents germination (Rick and Bowman 1961). Before sowing, the seeds were rinsed with tap water. Upon emergence of roots the seeds were transferred to vermiculite. Young seedlings bearing one or two leaves were transferred to aerated Hoagland solution, 20 seedlings per container of 22 litres. The solution contained (mg l^{-1}): $Ca(NO_3)_2 \cdot H_2O$, 1235; KNO_3, 535; $MgSO_4 \cdot 7H_2O$, 525; KH_2PO_4, 145; Sequestrene 138 Fe, 50; H_3BO_3, 2·9; $MnCl_2 \cdot 4H_2O$, 1·8; $ZnCl_2$, 0·12; $CuCl_2 \cdot 2H_2O$, 0·048; $H_2MoO_4 \cdot H_2O$, 0·04. Salt treatment was initiated at the 3–4 leaf stage by adding NaCl (25-mequiv. l^{-1} day^{-1} doses) to the containers of the salt-treated plants up to a final concentration of 100 or 150 mequiv. l^{-1}. Control plants remained in Hoagland solution.

Stem Elongation Rate

The length of the main stem was measured on the day on which salt was first added (day 0) and then at 3-day intervals to day 15. Stem growth was measured by expressing the length at each time interval as a percentage of the length at day 0. Elongation rate was calculated from the slope of the regression line between stem growth (Y) and time (X). The measurements included eight plants in each species–treatment combination.

Succulence and Accumulation of Ions

Succulence and ion content were determined 12 days after the last addition of salt in the top of the shoot (including the meristem and the very small leaves), the youngest fully expanded leaf, the middle section of the stem, and the proximal part (about 20 mm) of the main root in VF, H, Lc, Sp, and Lp, and only in the youngest fully expanded leaf in VF, H, Lc, Sp, and F_1 hybrids. Fresh material was weighed immediately after excision and again after oven-drying at 85°C for 24 h, and succulence was calculated as the ratio fresh weight:dry weight. The roots were rinsed for 5 min in a solution of 10 mM $CaSO_4$ and 0·5 M mannitol and blotted carefully before weighing.

Na^+, K^+, and Cl^- were determined in dried samples. The weighed dried samples were transferred to 3 ml of 0·1 M nitric acid for 72 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-EEL flame photometer. The measurements included three samples taken from three different plants in each species–treatment combination.

Results

Stem Elongation Rate

Stem elongation rate of both cultivators was higher than that of the wild plants under control conditions. Under salinity of 100 mequiv. l^{-1}, the rate decreased in all plants, the decrease being smaller in the wild species (Table 1).

Table 1. Elongation rate of the main stem of the cultivated tomato (VF, H) and its wild relatives (Lc, Sp, Lp) as affected by 100 mequiv. l^{-1} NaCl

The values represent the slope of the regression line between stem growth and time $\pm t_{0.05} \cdot S_b$ (Snedecor and Cochran: for more details see Materials and Methods)

Plant type	Slope of regression line for: Control	NaCl	% of control
VF	0·24±0·03	0·12±0·01	50·0
H	0·21±0·03	0·09±0·00	42·8
Lc	0·10±0·01	0·09±0·00	90·0
Lp	0·16±0·00	0·11±0·00	68·7
Sp	0·17±0·02	0·10±0·02	58·8

The decrease of elongation rate under salinity in three of the F_1 hybrids, VF×Sp, H×Sp, and H×Lc, was smaller than in the cultivated parents. The rate decreased similarly in the two cultivars and the hybrid VF×Lc (Table 2).

Table 2. Elongation rate of the main stem of the cultivated tomato (VF, H), its wild relatives (Lc, Sp), and F_1 hybrids as affected by 150 mequiv. l^{-1} NaCl

Other details are as in Table 1

Treatment	Elongation rate VF	H	Lc	Sp	VF×Lc	VF×Sp	H×Lc	H×Sp
Control	0·39 ±0·11	0·28 ±0·07	0·16 ±0·04	0·15 ±0·03	0·27 ±0·07	0·41 ±0·12	0·35 ±0·12	0·48 ±0·15
Salt-treated	0·15 ±0·03	0·11 ±0·01	0·10 ±0·02	0·07 ±0·01	0·11 ±0·02	0·20 ±0·03	0·17 ±0·03	0·25 ±0·07
% of control	38·5	39·3	62·5	46·7	40·7	48·8	48·6	52·1

Succulence

In all four species, the ratio fresh weight:dry weight was the highest in the stem, lower in the root, and the lowest in the leaf (Table 3). Among the wild species, Sp was the most succulent in all its major parts under both control and saline conditions. Lp was the least succulent except in the leaf. Salinity increased succulence most noticeably in leaves of Sp and decreased it in the tops of the cultivars.

Succulence was higher in the VF×Lc and VF×Sp hybrids than in the VF parent, and similar in H×Lc and H×Sp to that of the H parent (Table 4). Under salinity, the succulence increased in the wild parents and the four F_1 hybrids but remained unchanged in the two cultivars. The increase in VF×Sp and H×Sp was similar to that in the Sp parent. The increase in VF×Lc and H×Lc was intermediate between the parental values.

Table 3. Responses of the cultivated tomato (VF, H) and its wild relatives (Lc, Lp and Sp) to 100 mequiv. l^{-1} NaCl

Values are given ±s.e.

Plant type	Data for plant parts: Root		Stem		Leaf		Top	
	Control	NaCl	Control	NaCl	Control	NaCl	Control	NaCl
				(*a*) Succulence (fresh wt/dry wt)				
VF	15·8±0·7	12·5±0·1	23·3±1·0	20·4±1·6	7·8±0·1	6·4±0·2	9·5±0·2	7·9±0·7
H	14·1±0·1	13·6±0·9	24·7±0·3	22·0±2·7	7·8±0·2	6·8±0·1	8·6±0·3	6·9±0·5
Lc	17·7±1·3	14·2±0·8	19·4±1·0	19·3±0·5	7·9±0·2	7·5±0·2	9·3±0·6	9·0±0·6
Lp	13·4±0·8	11·7±0·9	12·7±0·8	13·5±1·9	8·5±0·2	8·6±0·8	7·5±0·2	6·8±0·4
Sp	17·1±1·1	17·3±1·0	26·7±2·4	31·8±0·5	10·3±0·4	12·4±0·8	9·2±0·3	9·1±0·3
				(*b*) Sodium (mequiv. g^{-1} dry wt)				
VF	0·07±0·03	1·00±0·01	0·11±0·04	2·65±0·21	0·01±0·00	0·15±0·02	0·02±0·00	0·26±0·09
H	0·06±0·03	1·05±0·16	0·20±0·09	2·87±0·09	0·01±0·00	0·21±0·03	0·06±0·06	0·15±0·06
Lc	0·04±0·04	2·40±0·59	0·59±0·24	4·68±0·51	0·07±0·00	0·81±0·06	0·32±0·08	1·10±0·15
Lp	0·00±0·00	1·15±0·28	0·06±0·06	2·05±0·05	0·16±0·04	1·30±0·25	0·08±0·08	1·03±0·28
Sp	0·21±0·12	1·69±0·14	0·38±0·27	7·16±0·07	0·01±0·00	1·60±0·12	0·03±0·01	2·16±0·33
				(*c*) Chloride (mequiv. g^{-1} dry wt)				
VF	0·14±0·05	1·48±0·05	0·28±0·05	1·16±0·04	0·02±0·01	0·17±0·00	0·07±0·01	0·19±0·03
H	0·20±0·02	1·58±0·12	0·32±0·05	1·32±0·12	0·04±0·01	0·27±0·01	0·06±0·00	0·14±0·02
Lc	0·03±0·03	1·80±0·14	0·12±0·00	1·41±0·05	0·01±0·01	0·35±0·03	0·03±0·02	0·40±0·05
Lp	0·09±0·00	1·47±0·25	0·13±0·03	0·91±0·12	0·02±0·00	0·32±0·07	0·04±0·01	0·17±0·04
Sp	0·17±0·06	2·26±0·13	0·23±0·03	1·78±0·05	0·02±0·02	0·28±0·02	0·04±0·00	0·25±0·03

Accumulation of Ions

Sodium

In all four species, sodium concentration per unit dry weight increased under salinity; its content was the highest in the stem, lower in the root, and lowest in the leaf (Table 3). The wild species, and especially Sp, accumulated under salinity much more Na^+ than the cultivars; the differences between the species was most noticeable in the leaf and top.

Table 4. Succulence in leaves of the cultivated tomato (VF, H), wild species (Lc, Sp), and F_1 hybrids as affected by 150 mequiv. l^{-1} NaCl

Values are given ±s.e.

Treatment	Succulence (ratio fresh wt:dry wt):							
	VF	H	Lc	Sp	VF×Lc	VF×Sp	H×Lc	H×Sp
Control	7·4 ±0·1	8·1 ±0·2	9·0 ±0·1	10·6 ±0·3	8·5 ±0·2	8·8 ±0·1	8·8 ±0·2	8·8 ±0·3
Salt-treated	7·5 ±0·2	7·8 ±0·2	10·9 ±0·4	13·0 ±0·5	9·1 ±0·2	10·7 ±0·4	9·5 ±0·3	11·0 ±0·3
% of control	102·6	96·0	120·6	122·1	107·9	122·0	107·4	125·0

The accumulation of Na^+ in the leaves of the wild parents and the F_1 hybrids was higher than in the cultivated varieties (Table 6). The accumulation was lower than the midparental values in VF×Lc, VF×Sp, and H×Sp, and equal to it in H×Lc.

Table 5. Potassium content in root, stem, leaf and tops of plants of the cultivated tomato (VF, H) and its wild relatives (Lc, Lp and Sp) as affected by 100 mequiv. l^{-1} NaCl

Values are given ±s.e.

Plant type	Potassium content [mequiv. (g dry wt)$^{-1}$]					
	Root			Stem		
	Control	NaCl	% decrease	Control	NaCl	% decrease
VF	2·04±0·14	1·36±0·06	33·3	3·74±0·16	2·32±0·18	38·0
H	2·14±0·01	1·61±0·08	24·8	3·72±0·02	1·97±0·28	47·1
Lc	1·72±0·20	0·84±0·10	50·2	3·11±0·23	0·73±0·12	76·5
Lp	1·93±0·01	1·08±0·05	44·1	2·69±0·25	1·09±0·18	59·5
Sp	2·91±0·17	2·28±0·07	21·7	4·29±0·34	0·99±0·06	76·9
	Leaf			Tops		
	Control	NaCl	% decrease	Control	NaCl	% decrease
VF	1·28±0·03	1·01±0·04	21·1	1·56±0·02	1·36±0·10	12·6
H	1·19±0·03	0·93±0·01	21·9	1·31±0·06	1·26±0·08	3·8
Lc	1·22±0·06	0·81±0·05	33·6	1·48±0·16	0·97±0·03	34·5
Lp	1·11±0·04	0·72±0·04	35·1	1·28±0·05	0·95±0·03	25·8
Sp	0·57±0·05	0·43±0·02	24·6	1·43±0·02	1·23±0·06	14·0

Potassium

Potassium concentration in control plants was the highest in the stem, lower in the root and top, and the lowest in the leaf in all four species, similarly to the distribution of Na^+ in salt-treated plants (Table 5). Under control conditions, Sp stem and roots accumulated most K^+ among the species studied, but at the same time Sp leaves contained

the lowest concentration of K^+. Under salinity, the concentration of K^+ decreased in all major parts studied in all four species, the decrease being the greatest in the stem, smaller in the leaf and root, and the smallest in the top. In all parts, decreases in K^+ under salinity were greater in the wild than in the cultivated species.

K^+ concentration in the leaves of the VF×Sp and H×Sp hybrids was similar to that of Sp, while K^+ in VF×Lc and H×Lc hybrids was similar to that of the cultivated parents (Table 6). Under salinity, potassium content decreased in leaves of all plants; the decrease was, however, much greater in the wild species and in all F_1 hybrids.

Table 6. Content of Cl^-, Na^+, and K^+ in leaves of the cultivated tomato (VF, H), wild species (Lc, Sp) and F_1 hybrids as affected by 150 mequiv. l^{-1} NaCl

Values are given ±s.e.

Plant type	Content[A] (mequiv. g^{-1} dry wt) of: Cl^-	Na^+	K^+ content (mequiv. g^{-1} dry wt) Control	Salt-treated	% of control
VF	0·80±0·06	0·81±0·18	1·34±0·06	0·94±0·04	70·1
H	1·07±0·04	0·46±0·08	1·31±0·04	0·95±0·05	72·5
Lc	1·58±0·08	2·23±0·22	1·46±0·05	0·65±0·05	44·5
Sp	1·32±0·12	2·95±0·25	1·00±0·06	0·35±0·05	35·0
VF×Lc	1·18±0·08	1·21±0·15	1·30±0·04	0·70±0·06	38·5
VF×Sp	1·20±0·08	1·63±0·19	1·05±0·03	0·33±0·05	31·4
H×Lc	1·43±0·04	1·32±0·28	1·33±0·03	0·54±0·05	40·6
H×Sp	1·04±0·06	1·29±0·09	1·01±0·03	0·41±0·05	40·6

[A] Salt-treated plants only; control plants contained only trace amounts of Na^+ and Cl^-.

Chloride

Like Na^+, Cl^- concentration increased in all four plant types under salinity. Unlike Na^+, chloride content in NaCl-treated plants of all four species was the highest in the root, lower in the stem, and the lowest in the leaf and the top (Table 3). The greatest difference in Cl^- accumulation was found between the stem and the leaves. The accumulation of chloride in the root, stem, leaf and top was higher in Lc and Sp plants as compared with the two cultivars. Chloride accumulation was most noticeable in the root and stem in Sp and in the top in Lc.

Table 7. K^+:Na^+ and Cl^-:Na^+ ratios in different parts of the cultivated tomato (VF, H) and wild species (Lc, Lp and Sp) as affected by 100 mequiv. l^{-1} NaCl

Plant type	K^+:Na^+ Root	Stem	Leaf	Top	Cl^-:Na^+ Root	Stem	Leaf	Top
VF	1·4	0·9	10·0	4·7	1·5	0·4	1·1	0·7
H	1·6	0·7	9·0	13·0	1·5	0·5	1·3	0·9
Lc	0·3	0·1	1·6	0·9	0·7	0·3	0·4	0·4
Lp	0·9	0·5	0·8	1·0	1·3	0·4	0·2	0·2
Sp	1·3	0·1	0·4	0·5	1·3	0·2	0·2	0·1

The accumulation of Cl^- in the wild parents and the F_1 hybrids, except in H×Sp, was higher than in the cultivars (Table 6). The value of Cl^- accumulation in VF×Sp and H×Lc was higher than the midparental values, equal to it in VF×Lc and lower in H×Sp.

K^+:Na^+ and Cl^-:Na^+ Ratios

The ratios K^+:Na^+ and Cl^-:Na^+ in the root, stem, leaf and top of H, VF, Lc, Lp and Sp plants treated with 100 mequiv. l^{-1} NaCl are presented in Table 7. In all parts studied,

K^+:Na^+ ratio was larger in the cultivated than in the wild species; the greatest difference was found in the root and shoot in Lc and in the shoot, leaf and top in Sp.

The K^+:Na^+ ratio in the leaves was similar to that of the wild parent in the VF×Sp, H×Lc, and H×Sp hybrids and almost equal to the midparental value in VF×Lc (Table 8).

Cl^-:Na^+ ratio in the root and stem was similar in all four species, being greater than 1 (except in Lc) in the root and smaller than 1 in the stem (Table 7). The situation was different in the leaf and tops: while in the cultivated plants the ratio was close to 1, it was much lower than 1 in the wild plants.

The Cl^-:Na^+ ratio in the leaves was equal to that of the cultivated parent in VF×Lc, equal to the midparental value in VF×Sp, and lower in H×Lc and H×Sp (Table 8).

Table 8. K^+:Na^+ and Cl^-:Na^+ ratios in leaves of cultivated tomato (VF, H), wild species (Lc, Sp) and F_1 hybrids as affected by 150 mequiv. l^{-1} NaCl

	VF	H	Lc	Sp	VF×Lc	VF×Sp	H×Lc	H×Sp
K^+:Na^+	1·2	2·1	0·3	0·1	0·6	0·2	0·4	0·3
Cl^-:Na^+	1·0	2·3	0·7	0·4	1·0	0·7	1·1	0·8

Discussion

The wild relatives of the cultivated tomato, *L. cheesmanii*, *L. peruvianum*, and *S. pennellii*, are distinguished from the cultivated species by: (1) a lower absolute elongation rate of the stem under control conditions and a smaller relative decrease of this rate under high salinity; (2) a higher accumulation of Na^+, which was most pronounced in the leaf and top of the shoot; and (3) a greater decrease of K^+ content under salinity, especially in the stem and to a lesser extent in the leaf and the top.

A positive correlation between Na^+ accumulation and salt tolerance was reported previously in studies in which each of the wild species included here was studied separately (Tal 1971; Rush and Epstein 1976, 1981; Dehan and Tal 1978). This correlation was confirmed by the present results.

In contrast to the cultivated plants, all three wild species do not absorb K^+ selectively to Na^+ under high NaCl salinity. Consequently, their Na^+ content increases and K^+ content decreases more under this condition. The substitution of K^+ by Na^+ is clearly indicated by their distribution in the control and salt-treated plants, respectively. In all plant types studied, the relative distribution of K^+ in the major parts under control conditions is identical to the distribution of Na^+ under NaCl salinity. Rush and Epstein (1981), working with Lc accession 1401, suggested that the accumulation of Na^+ can be used as a key characteristic in the evaluation of potential germplasms in selection and breeding programs aimed at the improvement of the salt tolerance of the tomato.

The extent and nature of the physiological functioning of Na^+ in the wild relatives of tomato under salinity is still an open question. Another open question is how electrical neutrality is maintained in the leaves and tops of the wild species, in which the Cl^-:Na^+ ratio is much lower than 1.

While the two tomato cultivars resembled each other in most of their responses to salinity, differences were found between the responses of the wild species. Among the wild plants, Sp is distinguished by the high succulence of its major vegetative parts. Resulting from the dilution effect of succulence, Sp plants have the lowest concentration of Cl^- per unit fresh weight under salinity as calculated from Table 3. Similarly, this species accumulates the largest amount of Na^+ in the shoot and the largest amount of K^+ in the root, as expressed per unit of dry or fresh weight. Consequently, the ratio K^+:Na^+ in Sp relative to Lc and Lp plants is lowest in the shoot and highest in the root. A high succulence

can be also used as a key characteristic to evaluate the potential of hybrids containing Sp germplasm in selection and breeding programs for improved salt tolerance. Plants of the wild species Lp are the least succulent among the plants studied except in the leaf. Plants of Lc are distinguished by the higher concentration of chloride in their shoots under salinity.

In all five plant types, the relative degree of succulence in the various parts of the plant is positively correlated with the distribution of sodium, both being the highest in the stem, lower in the root and the lowest in the leaf and top. The relation between Na^+ and succulence, which was demonstrated previously in other investigations, was discussed by Rains (1972).

The dominance relations for the various characteristics between the parental species as expressed in the F_1 hybrids are presented in Table 9. In all of the F_1 combinations except for VF×Lc, the stem elongation rate under both control conditions and salinity

Table 9. Dominance relations in the F_1 hybrids between cultivated tomato (VF, H) and the wild species (Lc, Sp)

Het, heterosis; D ( ), dominance of the parental species in parentheses; I, intermediate expression; PD ( ), partial dominance of the parent in parentheses

Character	VF×Lc	VF×Sp	H×Lc	H×Sp
Elongation rate				
Control	I	D(VF)	Het	Het
NaCl-treated	PD(Lc)	Het	Het	Het
NaCl-induced decrease	D(VF)	D(Sp)	I	Het
Succulence				
Control	I	I	I	I
NaCl-treated	I	I	I	I
NaCl-induced increase	PD(VF)	D(Sp)	I	D(Sp)
Cl^- content				
Salt-treated	I	PD(Sp)	PD(Lc)	D(H)
Na^+ content				
Salt-treated	PD(VF)	I	I	PD(H)
K^- content				
Control	D(VF)	D(Sp)	D(H)	D(Sp)
NaCl-treated	PD(Lc)	D(Sp)	D(Lc)	D(Sp)
NaCl-induced decrease	D(Lc)	D(Sp)	D(Lc)	D(Sp)

was higher than in both parents, indicating heterosis (Allard 1960). The present results suggest a complete dominance of Sp over the cultivated parents with respect to the relative decrease of elongation rate and K^+ level and for the increase of the succulence under salinity. In contrast to Sp, Lc was dominant only for the relative decrease of K^+ under salinity.

Rick (1960) ascertained that 17 out of 30 morphological differences between *L. esculentum* and Sp showed dominance in the F_1 hybrid between them, 6 for the characteristics of the former and 11 for those of the latter parent. According to Dobzhansky (1951), clear dominance expression, which is common in intraspecific crosses, is an exception in interspecific crosses, mainly because of the high interaction of different modifier gene complexes of the two parental species. The high proportion of characters which show clear dominance in the cross between *L. esculentum* and Sp has been explained by their cross-compatibility, which indicates that a high proportion of modifier complexes

is common to the two species, and the finding that several of these morphological characters are controlled by a small number of genes (Tal 1967). Such an explanation might also be correct for the dominant expression of some of the characteristics studied here in the VF×Sp and H×Sp crosses.

Acknowledgment

This research was supported by a grant from the United States–Israel (Binational) Agricultural Research and Development Fund (BARD).

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Manuscript received 16 August 1982, accepted 13 December 1982

Corrigendum

Volume 9, Number 4

Comparison between osmotic and hydrostatic water flows in a higher plant cell: determination of hydraulic conductivities and reflection coefficients in isolated epidermis of *Tradescantia virginiana.*

Stephen D. Tyerman and Ernst Steudle

p. 477. Equation (10) was printed incorrectly. The correct equation is presented below:

$$\sigma_s = 1 - \frac{P_s \overline{V}_s}{L_p RT} - a_f$$