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Salt sensitivity and low discrimination between potassium and sodium in bean plants

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Abstract

Bean plants (*Phaseolus vulgaris*) were very sensitive to moderate concentrations of NaCl, showing a dramatic decrease in their K^+ content in the presence of this salt. Increasing the KCl content of the nutrient medium released the inhibitory effect of NaCl by increasing the K^+ content of the plants. Likewise moderate concentrations of KCl were toxic for bean plants because they produced a large K^+ loading. NaCl partially released this toxicity by inhibiting the K^+ loading. When compared to the moderately salt tolerant sunflower plants (*Helianthus annuus*), bean plants showed a lower capacity to discriminate between K^+ and Na^+, at high Na^+ levels, and an uncontrolled K^+ uptake at moderate concentrations of K^+. It is concluded that this low capacity of discrimination of the K^+ uptake system of bean plants in presence of Na^+ can account for by the NaCl sensitivity of bean plants.

Introduction

The growth of most terrestrial plants is inhibited by moderate concentrations of NaCl, and only very few species are able to grow at the NaCl concentration of sea water, in contrast with the large number of plants and microorganisms living in seas and oceans. The NaCl sensitivity of terrestrial plants is so significant that those able to grow at the NaCl concentration of the fluids bathing animal cells (150 m*M* Na^+) are called salt tolerant; so-called salt sensitive plants are inhibited by NaCl concentrations below 50 m*M* (Greenway and Munns, 1980; Lessani and Marschner, 1978). The growth inhibition of most terrestrial plants at the NaCl concentration of sea water can be explained by the absence of adaptative mechanisms which are necessary to tolerate the significant water deficit and ion excess prevailing at this NaCl concentration, but the low NaCl that inhibits sensitive plants does not impose neither a water deficit nor an ion excess whose tolerance requires special mechanisms of adaptation. Most likely, in these cases, either a physiological process is very sensitive to Na^+ or Cl^-, or a deficient transport system allows an excessive accumulation of Na^+ or Cl^- in the cytoplasm of the plant cells.

Several reports in recent years suggest that the characteristics of K^+ and Na^+ transports are determinant of the NaCl tolerance. In suspension cells of *Brassica napus*, increased tolerance to NaCl and LiCl arises by alteration of the K^+ uptake system (Lefebvre, 1989), and tobacco cell cultures show enhanced K^+ uptake capacity when adapted to NaCl (Watad et al., 1991). It is also clearly established that salt-tolerant genotypes of wheat translocate less Na^+ from roots to shoots than salt-sensitive genotypes (Davis, 1984; Schachtman et al., 1989). The involvement of a Na^+ efflux system in determining the NaCl tolerance of plants is not clearly established, but it cannot be ruled out. In fact, in yeast a phenotype of salt sensitivity can be produced by disrupting the genes encoding the P-ATPases (Haro et al., 1991) or the Na^+/H^+ antiport (Jia et al., 1992) involved in Na^+ efflux, and NaCl sensitive wild strains can be cured by transformation with plasmids carrying these genes.

Bean plants are sensitive to low concentrations of NaCl (Lessani and Marschner, 1978), and we report here that this sensitivity can be accounted for by the low K^+/Na^+ discrimination when the plants were exposed at moderately toxic Na^+ concentrations.

Materials and methods

Plant material

Phaseolus vulgaris (cv Kora, Eurosemillas, S.A., Córdoba, Spain) and *Helianthus annuus* (cv Sun-Gro 380, Eurosemillas, S.A.) seeds were surface sterilized in 0.5% NaOCl (1 min), and germinated under irrigation with 5 m*M* $CaCl_2$ in Vermiculite and Perlite, respectively. The nutrient solution for plants was prepared by adding the required amounts of KCl and NaCl to a Na^+-K^+-free nutrient solution base prepared as described by Benlloch et al. (1989). Five-day-old seedlings were transferred to the nutrient solution with the selected concentrations of KCl and NaCl, and grown for 14 days, as described elsewhere (Benlloch et al., 1989). A transfer to fresh solution of the same initial composition was made in day seven. Plants grown in 50 m*M* NaCl and 100 m*M* NaCl were adapted to these final concentrations by raising the NaCl concentrations in two or three steps at 24-h intervals: 25–50–100 m*M* steps. Na^+ plants were prepared by growing the seedlings for 9 days in a 50 m*M* NaCl/0.1 m*M* KCl nutrient solution. K^+-starved plants were prepared by growing the plants in limited amounts of K^+, as described by Benlloch et al. (1989).

Cation contents

Plants were removed from the nutrient medium, and the roots were washed in 150 mL of 5 m*M* $CaSO_4$ during 5 min to allow the exchange of the cell wall contents. Then roots and shoots were weighed independently, and frozen. The cations were extracted from the plant materials, and analyzed by atomic absorption spectrophotometry as described previously (Benlloch et al., 1989). The total content of cations per plant, and per gram of the plant fresh weight (root and shoot) are normally reported. The first form of expression is used to calculate the net gain or loss of cations, and the second to asses the cation concentrations in the plant. All reported data are means of four plants. Error standards are not reported but in all cases they were lower than 5% of the mean.

Table 1. Weights of bean and sunflower plants grown at different NaCl/KCl concentrations. Plants grown 14 days in nutrient solutions with the indicated concentrations of Na^+ and K^+

	Nutrient medium	Roots	Shoots	Total
Plants	NaCl/KCl m*M*	(g/plant)		(%)[a]
Bean	0/1	7.9	10.4	92 a
	0/5	7.9	12.1	100 a
	50/1	5.6	6.6	61 b
	50/5	5.9	9.4	77 c
	100/1	3.7	3.8	37 d
	90/10	6.3	6.6	64 b
Sunflower	0/1	11.4	13.9	93 ac
	0/5	11.6	15.9	100 a
	50/1	10.1	10.0	74 b
	50/5	10.8	12.6	86 c
	100/1	8.5	7.1	57 d
	90/10	9.1	8.9	66 b

[a] Values with different letters differ significantly (Duncan test, probability = 0.05).

$^{22}Na^+$ loss

$^{22}Na^+$ plants were prepared as Na^+ plants (50 m*M* NaCl/0.1 m*M* KCl) but using $^{22}Na^+$ labeled NaCl (37 GBq $mmol^{-1}$). After 9 days the plants were removed from the nutrient solution, half of them counted and the other half transferred to 50 m*M* NaCl/5 m*M* KCl nutrient solution (700 mL per plant) without label. After two days, the plants transferred to 50 m*M* NaCl/5 m*M* KCl were removed from the solution and counted.

Rb^+ influx

The initial rates of Rb^+ uptake were calculated from the time courses of the Rb^+ content, which were followed for 30 min after the Rb^+ addition to K^+-starved bean plants. As described by Benlloch et al. (1989) for sunflower plants, Rb^+ was added to the K^+ exhausted medium where the plants were growing (less than 0.2 μM K^+).

Table 2. Weight and K^+ content of bean plants at different NaCl/KCl concentration in the nutrient medium. Plants grown 14 days in nutrient solutions with the indicated concentrations of NaCl and KCl

Nutrient medium NaCl/KCl m*M*	Fresh weight g/plant	K^+ μmol/plant	K^+ mol/g FW
0/50	5.6	2030	360
5/50	9.1	2080	270
10/50	10.8	1750	190

Results

Background description of Na^+ and K^+ effects

The effects of NaCl on bean plants and sunflower plants depended on the K^+ concentration of the nutrient medium, at a non-limiting Ca^{2+} concentration (3.0 m*M* Ca^{2+}). Increasing KCl in the nutrient medium reduced the toxic effects of high concentrations of NaCl, provided that the Na^+/K^+ ratio was high. In Table 1 it can be observed that 50 m*M* NaCl/1 m*M* KCl was more toxic than 50 m*M* NaCl/5 m*M* KCl, and 100 m*M* NaCl/l m*M* KCl more toxic than 90 m*M* NaCl/10 m*M* KCl. Performing these experiments we found that K^+ showed specific toxicity for bean plants (e.g. 50 m*M* KCl was more toxic that 50 m*M* NaCl/l m*M* KCl, compare Tables 1 and 2). To check the inhibitory effect of KCl, we grew plants with KCl and variable concentrations of NaCl. Surprisingly, 100 m*M* KCl killed bean plants in only a few days, and 50 m*M* KCl reduced growth by more than 70% with reference to plants in 1 m*M* or 5 m*M* KCl. In both cases the toxic effects were partially reversed by NaCl. At 50 m*M* KCl, 5 m*M* NaCl produced a 60% increase of growth, and 10 m*M* NaCl produced almost a twofold increase (Table 2), but further increments of NaCl produced very little growth improvements. The basis of the KCl toxicity and its release by NaCl is out of the scope of this report, but it is clear that the KCl toxicity occurs concomitantly with a large K^+ loading of the plants. NaCl reduced the K^+ loading and probably by this effect it reduced the K^+ toxicity; other effects of Na^+ are unlikely because the uptake of Na^+ was not appreciable in these experiments (Table 2). In the moderately salt tolerant sunflower plants, (i) NaCl was less toxic than in bean plants (Table 1), and (ii) KCl was slightly toxic (100 m*M* KCl produced a 40% decrease in the weight of the plants, and this inhibition was almost entirely accounted for by the decrease of the water potential).

The toxic effect of NaCl on bean plants occurred concomitantly with an important reduction of the K^+ contents of plants, and with the increase of Na^+ in the roots. Even the total content of K^+ plus Na^+ in the shoots of inhibited plants was lower than the K^+ content of the plants grown in the absence of NaCl (Table 3). Because the inhibited plants were smaller, probably as a result of the coordination between K^+ content and growth (Cheeseman, 1989), this reduction in the cation contents of the shoots did not result in a significant decrease in the concentration of cations (total cation contents over fresh weights). Compared to bean plants, the K^+ content of sunflower plants was less sensitive to the presence of NaCl in the nutrient solution, but sunflower plants accumulated significantly higher amounts of Na^+ (compare in Table 3 the data at 50 m*M* NaCl in both kind of plants).

Na^+ plants

Since the most significant effect of the toxicity of NaCl in bean plants was the reduction of the K^+ content, we decided to compare the K^+ and Na^+ net movements in bean plants and in the moderately salt tolerant sunflower plants. However, the design of the experiments required to make the comparison presented some difficulties. If the two kinds of plants were grown at the same K^+ and Na^+ concentrations, they were in different physiological conditions (e.g. one inhibited and the other not), and if they were standardized at the same degree of growth inhibition, the K^+ and Na^+ concentrations in the nutrient medium had to be very different. In both cases making difficult the analysis of the results. To overcome this problem, we first standardized both kinds of plants to a similar Na^+ state, by growing them for nine days at 0.1 m*M* K^+ and 50 m*M* Na^+ (see Materials and methods section). Then these Na^+ plants were transferred to a nutrient solution with 50 m*M* NaCl/5 m*M* KCl, which was moderately toxic for bean plants, and almost non toxic for sunflower plants (see Table 1). The same kind of Na^+ plants were also grown on 5 m*M* KCl nutrient solution as a control. In these experiments, we followed the changes in the K^+ and Na^+ contents during 5 days.

Na^+ plants prepared as described were small, and presented a low K^+ content. The Na^+ concentration was high in the roots in both species, and also moderately high in shoots of sunflower plants (see the first datum point in Figure 3). However, Na^+ plants kept

Table 3. K^+ and Na^+ contents of bean plants and sunflower plants grown at different NaCl/KCl concentrations. Plants as in experiments of Table 1

Plants	Nutrient medium	Roots				Shoots			
	NaCl/KCl	Na^+	Na^+	K^+	K^+	Na^+	Na^+	K^+	K^+
	(m*M*)	μmol/plant	μmol/g FW	μmol/plant	μmol/g FW	μmol/plant	μmol/g FW	μmoll/plant	μmol/g FW
Bean	0/1	–	–	590	80	–	–	1100	110
	0/5	–	–	950	120	–	–	2300	190
	50/1	360	70	280	50	100	20	650	100
	50/5	450	80	380	70	50	10	1700	180
	100/1	470	130	130	40	90	10	410	60
	90/10	890	140	390	60	120	30	1100	170
Sunflower	0/1	–	–	600	50	–	–	1500	110
	0/5	–	–	1500	130	–	–	1400	90
	50/1	780	80	560	60	280	30	1500	150
	50/5	500	50	1100	110	210	20	1900	150
	100/1	890	100	390	50	190	30	1100	150
	90/10	530	60	1100	120	180	20	1400	150

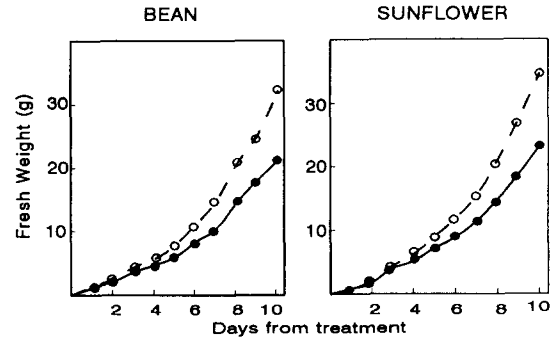

Fig. 1. Fresh weight gains of Na^+ bean-plants and Na^+ sunflower-plants after the transfer to 50 m*M* NaCl/5 m*M* KCl nutrient solution (•), and to 5 m*M* KCl nutrient solution (o). Data points are the means of the four plants, standard error lower than 5%. Weight of plants at the beginning of experiment: bean plants, 3.5 g; sunflower plants, 1.9 g.

a good growth capacity, and grew rapidly when transferred to 5 m*M* KCl or to 50 m*M* NaCl/5 m*M* KCl nutrient solutions (Fig. 1).

K^+ contents of Na^+ plants transferred to 5 mM KCl and to 50 mM NaCl/5 mM KCl

The total K^+ content of Na^+-plants increased almost linearly when they were transferred to 5 m*M* KCl, but the K^+ concentration in roots and shoots showed saturation courses because of the exponential growth of the plants (see K^+ per plant and expressed per gram in Figure 2). Differences between bean and sunflower plants were insignificant from all points of view except when the total K^+ taken up (kept in the roots and transferred to the shoots) was referred to the weight of roots (Fig. 2). The roots of sunflower plants showed a higher capacity of K^+ uptake (initial rate of 175 $\mu mol.g^{-1}.d^{-1}$ versus 100 $\mu mol.g^{-1}.d^{-1}$ in bean plants).

The addition of 50 m*M* NaCl to the 5 m*M* KCl nutrient medium decreased significantly the net K^+ uptake of bean plants, decreasing (30%) the net K^+ gain of the roots, but not the K^+ transferred to the shoots (see K^+ per plant in Figure 2). On the contrary, in sunflower plants 50 m*M* NaCl did not decrease the net K^+ gain of the roots at 5 m*M* KCl. In both types of plants, as a consequence of the normal K^+ transfer to the shoots, K^+ was more concentrated in the shoots of the plants growing with Na^+ because these plants were smaller (see K^+ per weight in Figure 2).

Na contents in Na^+ plants transferred to 5 mM KCl and to 50 mM NaCl/5 mM KCl

Na^+ bean-plants and Na^+ sunflower-plants lost Na^+ when transferred to the 5 m*M* KCl nutrient solution, exhibiting rate decreasing curves in the time courses of the Na^+ contents (see Na^+ content per plant in Fig. 3). The same type of curves occurred in the time courses of the Na^+ contents when referred to fresh weight, but

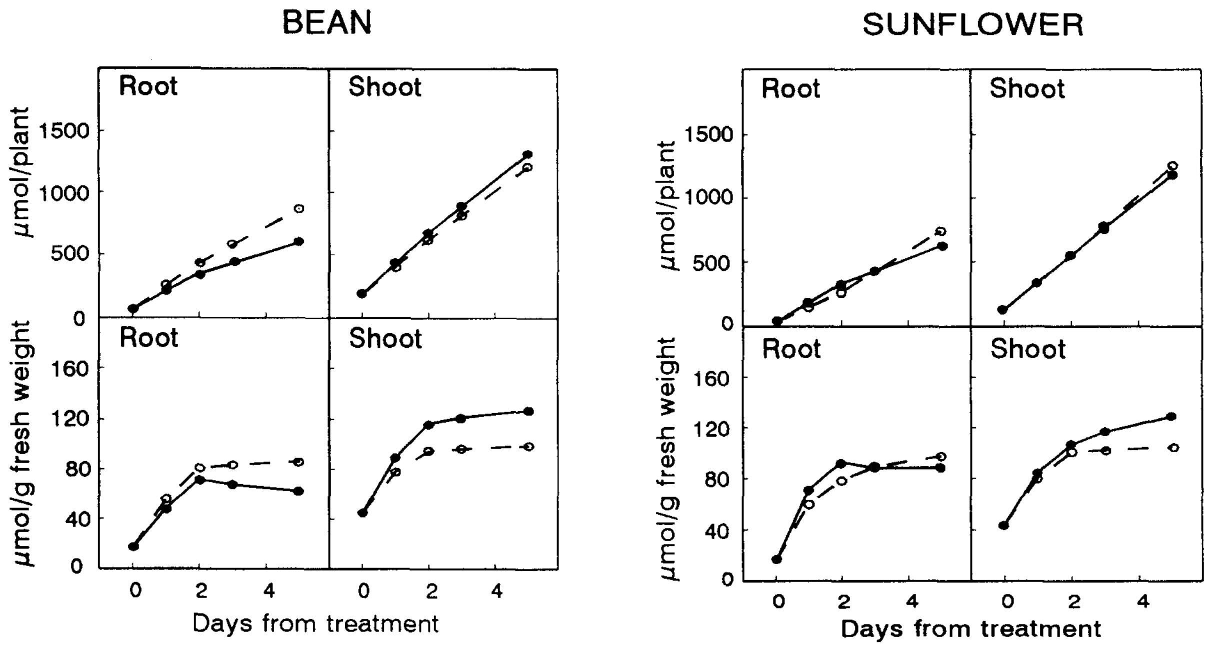

Fig. 2. Time courses of the K$^+$ contents of Na$^+$ plants after the transfer to 50 m*M* NaCl/5 m*M* KCl nutrient solution (•), and to 5 m*M* KCl nutrient solution (○). K$^+$ contents are expressed per plant, and per gram of fresh weight. Data points are means of four plants, standard error lower than 5%.

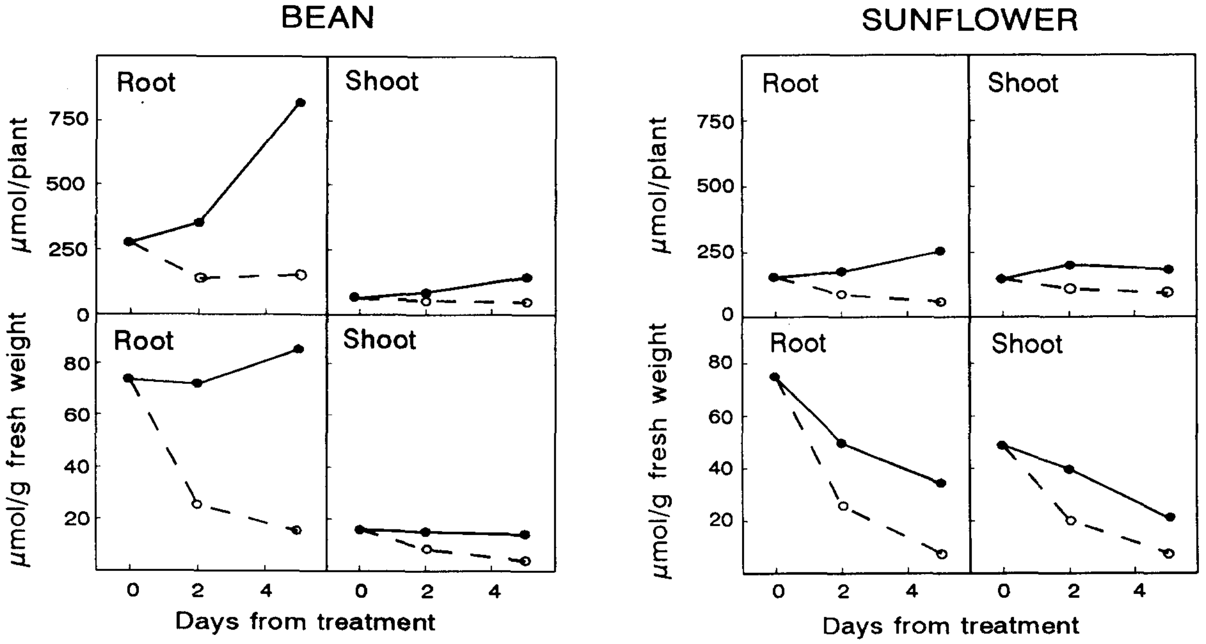

Fig. 3. Time courses of the Na$^+$ contents of Na$^+$ plants in the experiments of Figure 2. Plants transferred to 50 m*M* NaCl/5 m*M* KCl nutrient solution (•), and to 5 m*M* KCl nutrient solution (○). Data points are means of four plants, standard error lower than 5%.

in this case the apparent loss of Na$^+$ was more rapid because it was the result of both the net Na$^+$ loss and the growth of the plant. The data in Figure 3 suggest that the Na$^+$ loss and the growth of the plants were both similarly important for the decrease of the Na$^+$ concentration in Na$^+$ plants exposed to a Na$^+$-free medium (compare the decreases of the Na$^+$ contents expressed per plant and per gram). Na$^+$ losses in bean

Table 4. $^{22}Na^+$ loss in $^{22}Na^+$ plants transferred to 50 m*M* KCl solution. Na^+ plants labeled with $^{22}Na^+$ were transferred to 50 m*M* NaCl/5 m*M* KCl nutrient solution

Plants	$^{22}Na^+$ in roots (cpm) Initial	day 2
Bean	99,500	34,500
Sunflower	121,700	32,100

plants and sunflower plants did not show important differences, except those resulting from the higher Na^+ content of sunflower plants.

The time courses of the total Na^+ contents of Na^+ plants transferred to 50 m*M* NaCl/5 m*M* KCl changed completely with reference to the same plants transferred to 5 m*M* KCl. Net losses in the absence of Na^+ changed into net gains in its presence (Na^+ contents per plant in Figure 3). This was the result of the Na^+ uptake that occurred in the presence of Na^+, and not due to the inhibition of the efflux of Na^+. Consistent with previous results (Jacoby, 1979), experiments with ^{22}Na plants proved that Na^+ loss was not inhibited by external Na^+ (compare the Na^+ loss in 5 m*M* KCl in Figure 3 with $^{22}Na^+$ loss in Table 4).

Comparison of the time courses of the total Na^+ contents of bean plants and sunflower plants in 50 m*M* NaCl (Na^+ content per plant in Figure 3) showed that bean plants gained much more Na^+ than sunflower plants (530 Na^+ μmol per plant versus 100 Na^+ μmol per plant respectively). When the Na^+ content was referred to fresh weight it was clear that in sunflower plants the Na^+ concentration decreased while in bean plants did not. This was obviously the consequence of the large net gain of Na^+ in bean plants. Dilution by growth compensated the large net gain of Na^+, keeping constant the concentration of Na^+, but it was not sufficient to reduce it, as in sunflowers plants.

Kinetics of Rb^+ influx in bean plants

Na^+ bean-plants transferred to 50 m*M* NaCl/5 m*M* KCl took up more Na^+ than sunflower plants in the same conditions. This response, and the observed uncontrolled K^+ uptake at high KCl, indicated a distinctive function of the K^+ uptake system of bean plants, when it was compared to the K^+ uptake system of sunflower plants. A kinetic analysis of Rb^+ influx in K^+-starved bean plants showed a typical biphasic kinetics (not shown). However, compared to sunflower plants (Benlloch et al., 1989) the Km's in both phases were higher in bean plants (40 μ*M* Rb^+ versus 6 μ*M* Rb^+, and 32 m*M* Rb^+ versus 9 m*M* Rb^+). It may be also significant that the Vmax of the first phase was also lower in bean plants (4.7 μmol g^{-1} h versus 18 μmol g^{-1} h).

Discussion

The NaCl sensitivities of bean plants and sunflower plants were functions of the K^+ concentration in the nutrient medium. This notion cannot be explained by a Ca^{2+} defect because the experiments reported here were performed at a Ca^{2+} concentration (3 m*M*) sufficient to rule out a Ca^{2+} deficiency (Lahaye and Epstein, 1971). Furthermore, a Ca^{2+} deficiency should have produced a Na^+ content in the shoots higher than that found (Lahaye and Epstein, 1971). The reduction of the NaCl sensitivity by K^+ (Table 1) suggests that the inhibition of K^+ uptake in the presence of Na^+ may be the cause of NaCl toxicity (Cramer et al., 1987; Lynch and Läuchli, 1984). The K^+ content of sunflower plants was less sensitive to the external Na^+, and this may explain the higher salt tolerance of sunflower plants (Jeschke, 1984, and references therein). Considering our results with bean plants (Table 3), the presence of NaCl in the nutrient medium decreased the weight of the plants, the K^+ contents of the shoots and Na^+ replaced a part of the K^+ content of roots, but the K^+ concentration of shoots (K^+ content over weight) did not change. These results can be interpreted in two different ways: either the reduction of K^+ uptake produced the weight decrease or the decrease in the K^+ content was the consequence of the lower weight, which was primarily inhibited by the presence of Na^+. Present results do not allow to distinguish between these two possibilities. Which is clear is that bean plants took up much more Na^+ than sunflower plants when both types of plants were exposed to 50 m*M* NaCl/5 m*M* KCl (Fig. 3).

In contrast with the inefficient function of the K^+ uptake system, the Na^+ efflux system of bean plants was efficient in the presence of Na^+. The study of the Na^+/K^+ exchange in Na^+ bean-plants transferred to 5 m*M* KCl and to 50 m*M* NaCl/5 m*M* KCl showed clearly, and consistently with previous results (Jacoby, 1979), that Na^+ loss was not inhibited by the presence of 50 m*M* NaCl in the nutrient medium. Also consistent with previous results (Lessani and Marschner, 1978), the comparison of the Na^+ losses in bean plants and sunflower plants failed to reveal any significant difference that could account for the Na^+ sensitivity of bean plants.

Bean plants took up more Na^+ than sunflower plants, and Rb^+ at a lower rate and with lower affinity, but the kinetics of Rb^+ influx in bean plants exhibited a typical biphasic rate-concentration plot not very different from that exhibited by sunflower plants (Benlloch et al., 1989). The poorer discrimination between K^+ and Na^+ in bean plants might be explained because the ratio between Km_2/Km_1 in bean plants is lower than in sunflower plants. In fact, Na^+ is absorbed with low affinity even in low-salt roots (mechanism 2 in Rains and Epstein, 1967).

Besides the low K^+/Na^+ discrimination, the K^+ uptake system of bean plants seems to be poorly regulated. Plants in 5 m*M* KCl increased their K^+ content very much with reference to plants in 1 m*M* KCl, and plants in 50 m*M* KCl were dramatically loaded of K^+. In barley, K^+ influx is regulated by the K^+ content in root cells (Siddiqi and Glass, 1987), and the same probably occurs in many other plants. In bean plants this mechanism of control seems to fail. If the regulation of K^+ influx is due to an allosteric effect of internal K^+ on this system (Glass, 1976), the defective regulation and the low K^+/Na^+ discrimination could be both accounted for by the same protein. However, these two defects may be independent because the regulation of K^+ influx may follow a more complicated pathway than the allosteric response of the uptake system (Ramos et al., 1990).

It is attractive that in bean plants, and probably in others, salt sensitivity is the result of a low K^+/Na^+ discrimination of the K^+ uptake system, because modification of this system may be feasible in a near future.

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References

Benlloch M, Moreno I and Rodríguez-Navarro A 1989 Two modes of rubidium uptake in sunflower plants. Plant Physiol. 90, 939–942.

Cheeseman J M 1989 The adjustment of growth and K^+ transport in *Helianthus annuus* during salinization. *In* Plant Membrane Transport. Eds. J Dainty, M I DeMichelis, E Marre and F Rasi-Caldogno. pp 663–666. Elsevier Science Publishers, New York.

Cramer G R, Lynch J, Läuchli A and Epstein E 1987 Influx of Na^+, K^+ and Ca^{2+} into roots of salt-stressed cotton seedlings. Effect of supplemental Ca^{2+}. Plant Physiol. 83, 510–516.

Davis R F 1984 Sodium fluxes in intact roots of wheat varieties differing in salt tolerance. *In* Membrane Transport in Plants. Eds. W J Cram, K Janecek, R Rybova and K Sigle. pp 489–490. John Wiley and Sons, New York.

Glass A D M 1976 Regulation of potassium absorption in barley roots. An allosteric model. Plant Physiol. 58, 33–37.

Greenway H and Munns R 1980 Mechanisms of salt tolerance in nonhalophytes. Annu. Rev. Plant Physiol. 31, 149–190.

Haro R, Garciadeblas B and Rodríguez-Navarro A 1991 A novel P-type ATPase from yeast involved in sodium transport. FEBS Lett. 291, 189–191.

Jacoby B 1979 Sodium recirculation and loss from *Phaseolus vulgaris* L. Ann. Bot. 43, 741–744.

Jeschke W D 1984 K^+-Na^+ exchange at cellular membranes, intracellular compartmentation of cations, and salt tolerance. *In* Salinity Tolerance in Plants. Strategies for Crop Improvement. Eds. R C Staples and G H Toenniessen. pp 37–66. John Wiley and Sons, New York.

Jia Z P, McCullough N, Martel R, Hemmingsen S and Young P G 1992 Gene amplification at a locus encoding a putative Na^+/H^+ antiporter confers sodium and lithium tolerance in fission yeast. EMBO J. 11, 1631–1640.

Lahaye P A and Epstein E 1971 Calcium and salt tolerance by bean plants. Physiol. Plant. 25, 213–218.

Lefebvre D D 1989 Increased potassium absorption confers resistance to group IA cations in rubidium-selected suspension cells of *Brassica napus*. Plant Physiol. 91, 1460–1466.

Lessani H and Marschner H 1978 Relation between salt tolerance and high-distance transport of sodium and chloride in various crop species. Aust. J. Plant Physiol. 5, 27–37.

Lynch J and Läuchli A 1984 Potassium transport in salt-stressed barley roots. Planta 161, 295–301.

Rains D W and Epstein E 1967 Sodium absorption by barley roots: its mediation by mechanism 2 of alkali cation transport. Plant Physiol. 42, 319–323.

Ramos J, Haro R and Rodríguez-Navarro A 1990 Regulation of potassium fluxes in *Saccharomyces cerevisiae*. Biochim. Biophys. Acta 1029, 211–217.

Schachtman D P, Bloon A J and Dvorak J 1989 Salt-tolerant *Triticum* x *Lophopyrum* derivatives limit the accumulation of sodium and chloride ions under saline stress. Plant Cell. Environ. 12, 47–55.

Siddiqi M Y and Glass A D M 1987 Regulation of K^+ influx in barley: evidence for a direct control of influx by K^+ concentration of root cells. J. Exp. Bot. 38, 935–947.

Watad A E A, Reuveni M, Bressan R A and Hasegawa P M 1991 Enhanced net K^+ uptake capacity of NaCl-adapted cells. Plant Physiol. 95, 1265–1269.

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