PHYSIOL. PLANT. 65: 460–466. Copenhagen 1985

Short term $^{22}Na^+$ and $^{42}K^+$ uptake in intact, mid-vegetative *Spergularia marina* plants

John M. Cheeseman, P. D. Bloebaum and Linda K. Wickens

Cheeseman, J. M., Bloebaum, P. D. and Wickens, L. K. 1985. Short term $^{22}Na^+$ and $^{42}K^+$ uptake in intact, mid-vegetative *Spergularia marina* plants. – Physiol. Plant. 65: 460–466.

Spergularia marina (L.) Griseb. is a rapidly growing, annual, coastal halophyte. Because of its small size, it is suitable for isotope studies of ion transport well beyond the seedling stage. The purpose of this report is to establish the similarities and differences between $^{22}Na^+$ and $^{42}K^+$ uptake in *S. marina* and in more commonly used mesophytic crop species. Vegetative plants were used 18 days after transfer to solution culture. Plants were grown either on Na^+-free medium or on 0.2 × sea water.
$^{22}Na^+$ uptake was linear with time for several hours. The rate was relatively insensitive to external concentration between 1 and 180 mol Na^+ m^{-3}, particularly in Na^+-free plants. Transport to the shoot accounted for 40 to 70% of the total uptake, dependent on salinity but largely independent of time. $^{42}K^+$ uptake decreased with increasing salinity in Na^+-free plants and increased in 0.2 × sea water plants. Both uptake and transport to the shoot were non-linear with time, upward concavity suggesting recovery from a manipulative and/or osmotic injury. Steady state root contents were compared with predicted contents based on cortical cell electrical potentials using the Nernst equation. Reasonable agreement was found in all cases except Na^+ content of 0.2 × sea water plants, in which active efflux was indicated. Uptake studies conducted in the presence of chemical modifiers (dicyclohexylcarbodiimide, dinitrophenol and fusicoccin) showed responses of $^{42}K^+$ uptake as expected from studies on agronomic species, and implied the presence of a similar active uptake here despite the appearance of equilibrium. Active Na^+ uptake was suggested at low Na^+ levels. We conclude that *S. marina* is a promising experimental system combining the rapid nutrient acquisition strategy of agronomically important annuals with a high degree of salt tolerance.

Additional key words – Halophyte, ion transport, salinity tolerance.

J. M. Cheeseman (reprint requests) and L. K. Wickens, Dept of Plant Biology, Univ. of Illinois, 289 Morrill Hall, 505 S. Goodwin Avenue, Urbana, IL 61801, U.S.A.; P. D. Bloebaum (present address), Basic Sciences Division, Univ. of the Pacific, 2155 Webster Street, San Francisco, CA 94115, U.S.A.

Introduction

Recent studies of ion uptake by intact, fully autotrophic plants beyond the seedling stage have indicated the need for greater use of such plants in studies of ion acquisition, with less reliance on extrapolation of transport models developed using very young, nutrient-starved seedlings (Drew et al. 1984, Drew and Saker 1984, Erdei et al. 1984, Jensén and Pettersson 1984, Cheeseman 1985). It is also clear from discussions such as that of Chapin (1980) that our knowledge of basic transport physiology in higher plants is based largely on agronomic species. Relatively little is known about transport in wild species with differing nutrient acquisition strategies. Further study of such plants may prove both interesting and useful in understanding and improving tolerance to salt and other edaphic stress conditions in crop plants.

In previous reports (Cheeseman and Enkoji 1984, Cheeseman et al. 1985) we have described some of the

Received 16 July, 1985

characteristics of *Spergularia marina* (L.) Griseb. with regard to growth, morphology of vegetative plants and Na^+ and K^+ contents which indicate that it might be a promising experimental organism. As a small, rapidly growing annual coastal halophyte, *S. marina* is faced with a nutrient acquisition problem between that of ruderal species (growing with a high level of nutrient resources in general and a high frequency of disturbance) and stress tolerant species (growing under conditions of high salinity).

In this study we consider the short-term uptake of $^{42}K^+$ and $^{22}Na^+$ with emphasis on plants grown in Na^+-free, 0.1 × sea water medium (designated Na-0) and on plants grown on 0.2 × sea water medium, giving the level of maximal growth (Cheeseman et al. 1985). Electrophysiological characteristics of root cortical cells and reponses of uptake and cell potentials to chemical modifiers are considered for their indications of the metabolic basis for the selectivity of uptake for K^+ over Na^+. The results indicate broad similarities in basic transport characteristics between *S. marina* and the more commonly studied crop species. *S. marina,* however, maintains a high level of K^+ transport activity even under complete nutrient culture conditions. This, in combination with effective exclusion of Na^+ at high salinity, contributes fundamentally to the success of this species in its natural habitat.

Abbreviations – DCCD, dicyclohexylcarbodiimide; DNP, 2,4-dinitrophenol; FC, fusicoccin; ψ, root cortical cell potential.

Materials and methods

Spergularia marina seeds were collected from seed plants maintained in our growth chambers; the original source of the seeds was the salt marsh at Kincardine Bridge on the Forth River, Scotland. Germination and growth procedures and culture conditions were outlined in detail in the previous report (Cheeseman et al. 1985). For this study, mid-vegetative *S. marina* plants were used 17 to 19 days after transfer to solution cultures and 7 to 9 days after the start of salinization (if any).

Composition of the nutrient media was also as described previously (Johanson and Cheeseman 1983) and was based on dilutions of artificial sea water supplemented with nitrogen and phosphate. The 0.2 × sea water medium contained (in mol m^{-3}): KNO_3, 1.5; $KHCO_3$, 0.53; $CaCl_2$, 2.1; $MgSO_4$, 6.4; $MgCl_2$, 4.6; $(NH_4)H_2PO_4$, 1.0; NaCl, 90; micronutrients and Fe. Na-0 designates a 0.1 × dilution of complete sea water but without NaCl (in previous reports we have referred to this solution as "fresh water"); "1/1" designates the Na-0 medium supplemented with 1 mol NaCl m^{-3}. This designation indicates that both Na^+ and K^+ were present at 1 mol m^{-3}.

Following the growth period, the large styrofoam islands used to support the plants (Cheeseman et al. 1985) were broken along pre-scored lines and each of six smaller islands was transferred either directly to labeled medium at the appropriate time to initiate uptake experiments or, if the uptake medium was of lower salinity than the growth medium, to the first of two, 5 min rinses in unlabeled "uptake" medium. All experiments were performed in the growth chamber. For most experiments, labeled solutions were in plastic boxes slightly bigger than the foam islands; volume was 300 ml, and solutions were continuously aerated. For the time courses illustrated in Figs 1a and 2, the experiment was performed in the same size tray (4 l capacity) as was used for growth. Upon removal from the labeled medium, plants were rinsed for 3.5 min in two changes of ice-cold 20 mol $CaCl_2$ m^{-3}. Each sample consisted of 2 plants of very similar size. Plants were divided into roots, leaves and root/shoot interface, and weighed into vials for counting. Interfaces represented less than 5% of the total fresh weight of the plants. They showed accumulations of neither Na^+ or K^+ which might suggest them to play a role in salt exclusion such as that shown in mesophytes (e.g. Johanson and Cheeseman 1983). Separate harvest of interfaces was convenient to assure that no "root" component was included with "shoots" and vice versa. As they provided no further information, interfaces will not be considered further.

Uptake solutions were labeled with $^{22}Na^+$ (New England Nuclear) and $^{42}K^+$ (locally irradiated) as previously described (Johanson and Cheesman 1983). Samples were counted in one of two ways, with no difference in results. The first method used a Beckman LS-230 scintillation counter after ashing, and samples were recounted following decay of $^{42}K^+$. The second method used an LKB Compugamma gamma counter. In this method, no sample preparation was required after harvesting and weighing. Cross channel spillover, decay corrections, and conversion of counts to μmol Na^+ and K^+ were performed by processors internal to the counter.

In experiments using chemical modifiers, the following conditions were altered. For DCCD experiments, plants were pretreated with 50 mmol DCCD m^{-3} in 0.5% ethanol for 10 min; the inhibitor was applied in unlabeled growth solution. Time and concentration analyses were performed to identify these conditions; continued exposure to DCCD for a 2 h uptake was often found to result in wilting of the plants. DNP was also used at a concentration of 50 mmol m^{-3} (0.5% ethanol), but was added directly to the uptake medium from the start of the labeling period. pH was unchanged at 6.8. FC was used at 10 mmol m^{-3} (0.5% ethanol), again from the start of the uptake period. Concentrations and application conditions were chosen for DNP and FC based upon typical conditions in the literature and local experience in their use on other species. Control treatments paralleled modifier treatments using plants grown in the same tray.

Root cortical cell potentials were recorded using plants mounted intact in a recording chamber. The

chamber was inclined at an angle of 45° such that solution could be flowed continuously over the roots and could be changed rapidly. During the recordings, the plants were illuminated with an incandescent flood lamp filtered through 10 cm of water. Photosynthetic photon flux density at the plant level was similar to that in the growth chamber, 500 μmol quanta m^{-2} s^{-1}. For recordings using FC, roots were given a 15 min pretreatment in 10 mmol FC m^{-3} growth medium to minimize FC usage. Previous studies with FC have shown its action to be essentially irreversible and no indications to the contrary were observed in this study. For DCCD and DNP studies, inhibitors were added directly to the recording medium and changes of potential were recorded during their action. The remainder of the electrophysiological apparatus was that previously used (Cheeseman and Hanson 1979).

Statistical analyses were performed using the BMDP Statistical Software package (Dixon 1981).

Results

Table 1 summarizes the 2 h uptake rates of $^{22}Na^+$ and $^{42}K^+$ at various salinity levels by plants grown on either Na-0 or 0.2 × sea water medium at 18 days after transfer to solution culture. Also indicated is the percentage of the total isotope which was transported to the shoot during the period of labeling. $^{42}K^+$ uptake by Na-0 plants declined with increasing salinity at all levels, and in all cases was lower than uptake in the Na-0 medium. Root retention declined proportionately less, so that the percentage of the total label recovered in the shoots declined with increasing salinity. A specific effect of Na^+ on K^+ uptake at constant K^+ was implied by comparison of rates in the Na-0, 1/1 and 0.1 × sea water media which differed only in their NaCl contents. Both $^{22}Na^+$ uptake and the rate of transport to the leaves were less sensitive to salinity. From 1 to 180 mol Na^+ m^{-3}, uptake increased by less than a factor of 3.5, and the proportion of the total which was transported to the leaves was relatively constant.

Somewhat different results were found with plants grown on 0.2 × sea water medium. $^{42}K^+$ uptake increased with salinity. The similarity of K^+ uptake rates in Na-0 and in 0.01 × sea water medium (the latter with only one-tenth the total K^+) and the increase of K^+ uptake at 0.1 × sea water suggest a Na^+ stimulation of K^+ uptake under these conditions. $^{22}Na^+$ uptake was more sensitive to salinity than in the Na-0 grown plants, and the rate of Na^+ transport to the leaves was also higher.

The occurrence of transport to the shoot in the experiments summarized in Tab. 1 indicates that it was not simply the initial, unidirectional influx of Na^+ and K^+ which was being observed. For Na^+, however, the results were the same regardless of the experimental period. Figure 1a shows the time course of total uptake and root accumulation of $^{22}Na^+$ by plants grown in 0.2 × sea water with uptake periods ranging from 20 to 140 min. The rate of total uptake indicated by the slope was 14.4 μmol (g fresh $weight_{root}$)$^{-1}$ h^{-1}. Transport to the shoot, calculated from the ratio of the slopes, represented 75% of the total. Separate experiments have shown linearity of uptake to extend down to 45 s and up to 8 h. A similar pattern was found under other uptake conditions, as illustrated in Fig. 1b using Na-0 grown plants and 1/1 uptake medium. Total uptake was 6.9 μmol (g fresh $weight_{root}$) $^{-1}$ h^{-1}, with 67% of the total $^{22}Na^+$ label being transported to the shoots.

Tab. 1. Uptake of Na^+ ($^{22}Na^+$) and K^+ ($^{42}K^+$) and transport to the shoots in mid-vegetative *S. marina* plants grown in Na-0 and on 0.2 × sea water media. Uptake of labels was from media indicated; uptake period was 2 h. Rates are expressed as μmol (g FW_{root})$^{-1}$ h^{-1}. Transport is expressed as percentage of the total label in the plants. Data are means ± SEM (n).

Uptake medium	$[Na^+]^o$ (mol m^{-3})	$[K^+]^o$ (mol m^{-3})	Uptake		Transport	
			$^{22}Na^+$	$^{42}K^+$	$^{22}Na^+$	$^{42}K^+$
			Na-0 grown			
Na-0	0	1	–	6.7 ±0.2 (127)	–	39
1/1	1	1	4.9±0.1(339)	4.3 ±0.1 (322)	45	35
0.01×	4.5	0.1	11.3±0.3(26)	2.8 ±0.4 (34)	51	31
0.1×	45	1	14.1±1.3(47)	1.9 ±0.2 (51)	46	34
0.2×	90	2	17.0±0.6(16)	1.1 ±0.1 (16)	49	30
0.4×	180	4	21.8±0.4(46)	0.76±0.02(46)	39	16
			0.2 × sea water grown			
Na-0	0	1	–	1.1±0.1(24)	–	22
0.01 ×	4.5	0.1	2.4±0.2(6)	1.2±0.2(6)	57	36
0.1 ×	45	1	6.5±0.4(36)	2.9±0.4(36)	71	32
0.2 ×	90	2	14.4±0.4(237)	4.7±0.2(239)	65	45
0.4 ×	180	4	42.0±1.2(49)	7.4±0.2(49)	55	29

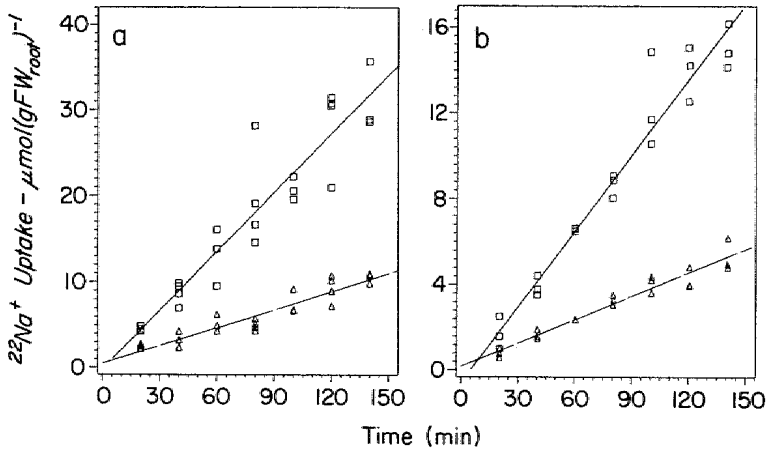

Fig. 1. The time course of $^{22}Na^+$ uptake (□) and root accumulation (△) by mid-vegetative *S. marina* plants grown on 0.2 × sea water (a) or on Na-0 medium (b). Uptake in (b) was from 1/1 medium. Each time course is the result of a single experiment. Lines were fitted by linear regression. Each point represents a single 2-plant harvest.

A constant rate of $^{42}K^+$ uptake, though occasionally found, was much less representative. The more usual time course is shown in Fig. 2. The experiment illustrated here again involved plants grown in 0.2 × sea water but very similar results were found under the other conditions of Tab. 1.

The slopes of the total uptake and root accumulation curves at 2 h in Fig. 2 were higher than the uptake per hour calculated from the content at 2 h by factors of 1.2 (total uptake) and 1.6 (root accumulation). The upward concavity of these curves suggests K^+ uptake was particularly sensitive to "injury", even simple transfer of plants to the uptake medium (cf. Chastain and Hanson 1981).

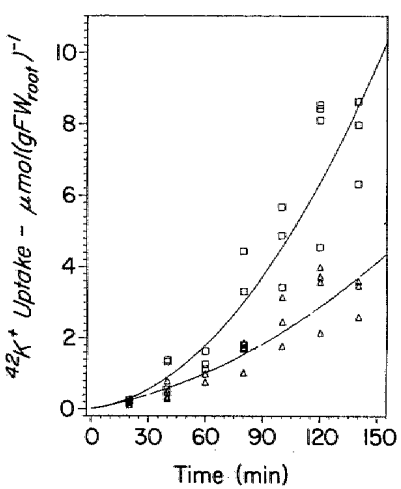

Fig. 2. The time course of $^{42}K^+$ uptake (□) and root accumulation (△) from 0.2 × sea water by mid-vegetative *S. marina* plants grown in the same medium. Each point represents a single 2-plant harvest. Lines are quadratic fits by polynomial regression. Goodness-of-fit tests indicated necessity and sufficiency of this degree. Data are from the same experiment as Fig. 1a.

In these experiments, plants were transferred, with at most a brief intervening rinse, directly from the growth medium to the labeled uptake medium. Therefore the results of Tab. 1 also include any artefact which might have arisen from the osmotic shock of the transfer. In parallel studies of root cell potentials, it was sometimes observed that cortical cells plasmolyzed with abrupt salinity changes, though recovery was rapid. Figure 3a shows an example of an experiment in which placement of the recording electrode was maintained during large salinity changes. Recovery of the potential to nearly the original level was complete within 10 min. Regardless of the rapid recovery of potential, however, it remains unclear whether the transport systems follow the same patterns, and we consider it not unlikely that some degree of osmotic effect is reflected in Tab. 1. Nevertheless, it is also interesting that two other halophytes in comparable experiments showed substantially different responses of $^{42}K^+$ uptake (Na-0 grown plants) to increasing salinity. *Plantago maritima* showed a small (1.5 fold) increase of K^+ uptake as solution strength was raised from 0.01 × to 0.4 × sea water and *Lycopersicon cheesmanii* showed a somewhat larger (4-fold) increase in $^{42}K^+$ uptake over the same range (J. M .Cheeseman and L. K. Wickens, unpublished results).

The steady potentials of the root cortical cells for Na-0 grown plants (with or without addition of 1 mol Na^+ m^{-3}) and for plants grown in 0.2 × sea water are summarized in Tab. 2. These values were used to calculate the cellular concentrations of Na^+ and K^+ which would be expected if electrochemical equilibrium were attained, and those calculations are compared in Tab. 2 with the actual root contents reported previously (Cheeseman et al. 1985). With the exception of Na^+ contents of plants grown in 0.2 × sea water, all calcu-

Tab. 2. The electrochemical status of Na^+ and K^+ in roots of mid-vegetative *S. marina* plants. Predicted root concentrations were calculated using the Nernst equation, measured cortical cell potentials and tissue ion contents with the assumption that all activity coefficients were equal. Root content data are from Cheeseman et al. 1985; n=10.

[a]) ψ in 1/1 grown plants assumed equal to ψ in Na-0 grown plants transferred to 1/1 during recording.

Growth medium	Recording medium	ψ (mV)	µmol (g FW)$^{-1}$			
			$[Na^+]_{root}$	$[K^+]_{root}$	$[Na^+_w]_{pred}$	$[K^+]_{pred}$
Na-0	Na-0	−121 ± 2 (59)	1.1 ± 0.3	103 ± 2	<11	112
	1/1	−108 ± 3 (29)	52 ± 3	97 ± 7	68[a])	68[a])
0.2 ×	0.2 ×	−106 ± 4 (20)	86 ± 1	82 ± 2	5600	125

Tab. 3. The effects of the chemical modifiers DCCD, DNP and FC on $^{22}Na^+$ and $^{42}K^+$ uptake by mid-vegetative *S. marina* plants grown on Na-0 or 0.2 × sea water medium. Values are percentage of control for whole plants and (figures in parentheses) for accumulation in roots.

Uptake medium		Modifier		
		DCCD	DNP	FC
Na-0	K^+	10 (13)	5 (4)	–
FW→1/1	K^+	13 (10)	4 (3)	146 (220)
	Na^+	36 (39)	15 (21)	109 (129)
0.2 ×	K^+	4 (4)	4 (5)	153 (280)
	Na^+	65 (72)	58 (40)	99 (110)

lated values were acceptably close to observed values, requiring less than a 10 mV change in cell potential for agreement.

Because such a large proportion of the total ion contents of the plants was in the shoots, and because transport of labels to the shoot was also rapid, it is not clear that these results require the existence of a Na^+ efflux pump to the medium in the 0.2 × grown plants, or preclude the existence of an active K^+ uptake system under any of the growth conditions. Therefore, we considered the effects of chemical modifiers on isotope uptake and cell potential in *S. marina*.

Table 3 summarizes the effects of 50 mmol m^{-3} DCCD or DNP and of 10 mmol FC m^{-3} on isotope uptake by Na-0 and 0.2 × sea water-grown plants. DCCD, which also rapidly reduced net H^+ efflux (Cheeseman and Enkoji 1984), reduced $^{42}K^+$ uptake by 90% regardless of growth conditions. $^{22}Na^+$ uptake was reduced twice as much at the lower external level as at the higher. Root accumulation (figures in parentheses) and total uptake were affected similarly.

DNP had similar effects on K^+ uptake. This effect was probably due to the action of the inhibitor on respiration rather than a direct effect on the permeability of the plasma membrane to K^+ or Na^+, as the pH was 6.8 (Jackson 1982). Na^+ uptake was again reduced more from 1/1 than from 0.2 × sea water medium.

FC, which strongly stimulated net H^+ efflux in both growth conditions, also increased $^{42}K^+$ uptake considerably. $^{22}Na^+$ uptake was unaffected in plants grown in 0.2 × sea water and was only slightly increased under 1/1 conditions. $^{42}K^+$ accumulation by the roots was increased proportionately more than was total uptake.

FC increased the cortical cell potential of Na-0 grown plants from the level shown in Tab. 2 to −148 ± 4 mV; the potentials of plants grown in 0.2 × sea water were increased to −141 ± 3 mV. Results using DCCD were more variable and seemed to depend on the level of the potential before addition of inhibitor (a similar result has also been observed in studies of low-salt corn roots (J. M. Cheeseman, unpublished data). Figure 3b and c illustrate the two typical responses. In the first case (Fig. 3b) the initial potential was low and inhibitor sensitivity was high. In the second (Fig. 3c), the initial potential was high and sensitivity low. In Na-0 grown plants the mean final potential with DCCD was −120 mV in those plants showing little response and −52 mV in those plants depolarizing.

Results with DNP were more consistent: in Na-0 and 0.2 × sea water grown plants, potentials were reduced to −64 ± 10 mV, and −76 ± 6 mV, respectively. Figure 3d and e illustrate the time course and reversibility of the response. The biphasic repolarization was similar to that seen in tomato leaf cells following treatment with cyanide and salicylhydroxamic acid (Cheeseman and Pickard 1977).

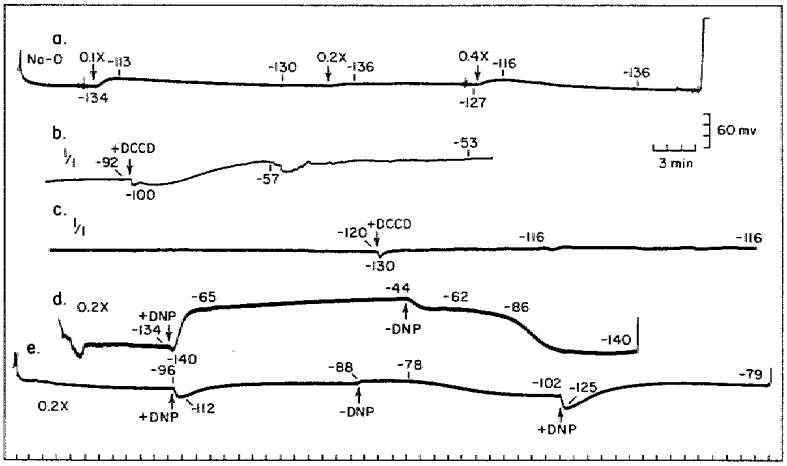

Fig. 3. The response of root cortical cell electrical potentials to changes of salinity and to inhibitors. (a) Response to increasing salinity in Na-0 grown plant. (b), (c) Responses to DCCD in Na-0 grown plants transferred to 1/1 medium prior to addition of inhibitor. Initial potential was "low" in (b) and "high" in (c). (d), (e) Response to DNP in 0.2 × sea water grown plants. Result in (d) illustrates the greatest initial potential and largest depolarization seen in 0.2 × plants, and indicates the reversibility of the inhibitor effect. (e) Illustrates the reproducibility of the effect in a single cell. Time ticks on horizontal axis are 1 min intervals. Arrows indicate times of inhibitor application or removal. Values are cell potentials (mV).

Discussion

In this paper we have considered the uptake of isotope-labeled Na^+ and K^+ by fully autotrophic vegetative *S. marina* plants grown on either Na^+-free medium or 0.2 × sea water. As would be expected based on the low Na^+/K^+ whole plant ratios previously reported, the results showed substantial selectivity in favor of K^+ uptake in the short term as well. There was, however, a discrepancy between the uptake ratios in Tab. 1 and content ratios (Cheeseman et al. 1985). This appears to be an artefact caused by the sensitivity of the K^+ uptake system to even gentle handling (Fig. 2). The discrepancy was reduced when slopes were compared at 2 h, and it disappeared when linear rates were compared over the 2 to 8 h uptake period, i.e. after the "recovery" (data not shown). This selectivity could be accomplished several ways, and inhibitor and electrophysiological experiments were conducted to aid in their resolution.

S. marina showed many transport characteristics similar to those of low-salt roots of mesophytes. Though K^+ was apparently near electrochemical equilibrium in root cortical cells, the K^+ uptake system responded to chemical modifiers in a manner similar to the same system in the more well studied plants. The effects of any of the modifiers were greater than would be expected based on changes in cell potential alone. Taken along with the previously reported characteristics of the H^+ extrusion system in *S. marina* (Cheeseman and Enkoji 1984), these results suggest that K^+ uptake was active and that the system was similar to that in mesophytes. If any difference were to be particularly noteworthy here, it would be that *S. marina* demonstrated the activity even without K^+ deprivation, unlike (for example) corn (Cheeseman and Enkoji 1984) or barley (Glass et al. 1981). Eggers and Jeschke (1984) have shown that the H^+/K^+ transport system is partially responsible for the selectivity in favor of K^+ in intolerant (*Fagopyrum*) and more tolerant (*Triticum*) mesophytes. In wheat, as in barley (Ratner and Jacoby 1976), a Na^+/K^+ exchange was also implied. Despite the possible stimulation of K^+ uptake by Na^+ in *S. marina* grown in 0.2 × sea water (Tab. 1) we have, as yet, no evidence regarding such an exchange in this species.

At low external Na^+ concentrations and with plants of low Na^+ status, the inhibitor sensitivity of Na^+ uptake was also somewhat greater than would be expected based on changes in cell potential alone, suggesting that active Na^+ accumulation may occur under those growth conditions. The suggestion is, however, less convincing than is the hypothesis that an active Na^+ exclusion system exists at higher concentrations. The electrochemical disparity shown in Tab. 2, together with the small depolarization and rapid repolarization of cortical cells following increases in external Na^+, suggests active and electrogenic Na^+ efflux. L'Roy and Hendrix (1980) showed similar electrochemical evidence for active Na^+ exclusion and a similar insensitivity of ψ to salinity in *Salicornia bigelovii*. We have reported a similar result for corn (Cheeseman 1982), in which case the suggestion was also supported by a disparity between long- and short-term $^{22}Na^+$ influx rates (indicating a high turnover rate of root Na^+). In the present study, however, $^{22}Na^+$ influx was linear for extended time periods.

It should be noted that the results reported here differ substantially from those reported by Jefferies (1973) who studied the slowly growing, perennial halophyte,

Triglochin maritima. The differences were particularly pronounced with regard to the Na^+ stimulation of K^+ uptake (which was pronounced in *T. maritima* under Na^+-free growth conditions), to the Na^+-induced depolarization of ψ, and to the insensitivity of K^+ uptake to the uncoupler CCCP (at high K^+ levels in *T. maritima*).

In conclusion, the similarities discussed above between *S. marina* and young crop plants should clearly not be taken as an indication that all wild species have the transport or nutritional characteristics of all crop species, but as an indication that this wild species, combining rapid nutrient acquisition with a high level of salt tolerance, may help us elucidate the underlying mechanisms of salt tolerance or sensitivity in plants.

Acknowledgments – The research was support by grants PCM 80-11138 and PCM 83-04417 from the National Science Foundation.

References

Chapin, F. S. 1980. The mineral nutrition of wild plants. – Annu. Rev. Ecol. Systematics 11: 233–260.

Chastain, C. J. & Hanson, J. B. 1981. Proton efflux from corn roots induced by tripropyltin. – Plant Physiol. 68: 981–982.

Cheeseman, J. M. 1982. Pump-leak sodium fluxes in low salt corn roots. – J. Membr. Biol. 70: 157–164.

– 1985. An effect of Na^+ on K^+ uptake in intact seedlings of *Zea mays*. – Physiol. Plant. 64: 243–246.

– & Enkoji, C. 1984. Proton efflux from roots of intact *Spergularia marina* plants. – J. Exp. Bot. 35: 1048–1052.

– & Hanson, J. B. 1979. Mathematical analysis of the dependence of cell potential on external potassium in corn roots. – Plant Physiol. 64: 1–4.

– & Pickard, B. G. 1977. Electrical characteristics of cells from leaves of *Lycopersicon*. – Can. J. Bot. 55: 497–510.

– , Bloebaum, P., Enkoji, C., Wickens, L. K. 1985. Salinity tolerance in *Spergularia marina*. – Can. J. Bot. 63: 1762–1768.

Dixon, W. J. (Chief Ed.) 1981. BMDP Statistical Software. – University of California Press, Berkeley, CA, USA. ISBN 0-520-04408-8.

Drew, M. C. & Saker, L. R. 1984. Uptake and long-distance transport of phosphate, potassium and chloride in relation to internal ion concentrations in barley: evidence of non-allosteric regulation. – Planta 160: 500–507.

– , Saker, L. R. Barber, S. A. & Jenkins, W. 1984. Changes in the kinetics of phosphate and potassium absorption in nutrient-deficient barley roots measured by a solution-depletion technique. – Planta 160: 490–499.

Eggers, H. & Jeschke, W. D. 1984. Proton fluxes and K^+/Na^+ selectivity in roots of intact wheat and buckwheat plants. – *In* Membrane Transport in Plants (W. J. Cram, K. Janáček, R. Rybová and K. Sigler, eds), pp. 394–395. Academia, Prague.

Erdei, L., Oláh, Z. & Bérczi, A. 1984. Phases in potassium transport and their regulation under near-equilibrium conditions in wheat seedlings. – Physiol. Plant 60: 81–85.

Glass, A. D. M., Siddiqi, M. Y. & Giles, K. I. 1981. Correlations between potassium uptake and hydrogen efflux in barley varieties. – Plant Physiol. 68: 457–459.

Jackson, P. C. 1982. Differences between effects of undissociated and anionic 2, 4,-dinitrophenol on permeability of barley roots. – Plant Physiol. 70: 1373–1379.

Jefferies, R. L. 1973. The ionic relations of seedlings of the halophyte *Triglochin maritima* L. – *In* Ion Transport in Plants (W. P. Anderson, ed.), pp. 297–321. Academic Press, London. ISBN 0-12-058250-3.

Jensén, P. & Pettersson, S. 1984. Influence of light and dark and the experimental design on kinetics of K^+(^{86}Rb) influx in roots of intact spring wheat. – Physiol. Plant. 60: 65–69.

Johanson, J. G. & Cheeseman, J. M. 1983. Uptake and distribution of sodium and potassium by corn seedlings. I. The role of the mesocotyl in "sodium exclusion". – Plant Physiol. 73: 153–158.

L'Roy, A. & Hendrix, D. L. 1980. Effect of salinity on cell membrane potential in the marine halophyte, *Salicornia bigelovii* Torr. – Plant Physiol. 65: 544–549.

Ratner, A. & Jacoby, B. 1976. Effect of K^+, its counteranion and pH on sodium efflux from barley root tips- – J. Exp. Bot. 27: 843–852.

Edited by S. Pettersson

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.