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Sodium and Potassium Compartmentation and Transport in the Roots of Intact Lettuce Plants[1]

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ABSTRACT

In this report, we consider the accumulation in roots, and transport to the shoot, of Na^+ and K^+ in intact lettuce plants (*Lactuca sativa* cv Black-seeded Simpson). Plants were grown in modified Hoagland medium supplemented with 10 moles NaCl per cubic meter. At this salinity, significant levels of Na^+ were accumulated in roots and shoots, but there was no reduction in plant growth. Transport characteristics for both Na^+ and K^+ were qualitatively similar to those previously reported, for *Spergularia marina*, indicating that the results obtained with these experimental protocols are not limited to one unconventional experimental plant. The most pronounced difference in transport of the two ions was evident when transport was followed in a chase period after a 10 minute uptake pulse. For Na^+, there was an initially rapid, but small, loss of label to the medium, and very little movement to the shoot. For K^+, little label was lost from the plants, but translocation to the shoot proceeded for at least 60 minutes. The transport systems were further distinguished by treating the roots during labeling with 20 micrograms per milliliter cycloheximide. For K^+, both uptake and translocation were reduced by about 50%. For Na^+, root accumulation was stimulated more than fivefold, while transport to the shoot was reduced about 20%. Cycloheximide also modified the Na^+ transport characteristics such that continued translocation occurred during the chase period of pulse-chase studies.

The effective management of Na^+ and K^+ is fundamental to the survival of any plant in a saline environment (4, 9). In two previous papers (12, 13), we have reported on ion compartmentation and partitioning in roots of the coastal halophyte, *Spergularia marina*. We suggested comparability to less tolerant, mesophytic species because of the similarity of their overall resource problems and reproductive strategies; *S. marina* is a rapidly growing annual, and it lacks salt glands or other specialized salt exclusion mechanism.

In those reports, we characterized the symplastic compartments responsible for transport of Na^+ and K^+ across the root. Our analyses indicated, at least for the halophyte, that traditional cytoplasm-vacuole models of cellular compartmentation were insufficient to account for the measured transport, compartmentation, and partitioning of the two ions, and that analysis techniques conventionally used were unlikely to identify such deficiencies (3).

In this paper, we report on comparable studies using lettuce, a mesophyte and important crop species, the cultivation of which has been affected by salinization (23). Plants were grown at a low level of salinity to avoid growth reductions or other indications of 'salt stress.' The species was chosen, as was *S. marina*, for its rapid growth rate, its simple root morphology, and the small amount of tissue involved in nonproductive support functions. For both Na^+ and K^+, the results indicate that our results for *S. marina* were not a peculiarity of that species.

MATERIALS AND METHODS

Lactuca sativa (cv Black-seeded Simpson) seeds were germinated in vermiculite moistened with growth solution and were transferred to hydroponic culture on the fifth day. All ages presented here refer to days after that transfer. The hydroponic arrangement was as described previously for *Spergularia marina* (5, 6), except that a MHS[3] was used instead of modified sea water. The growth solution contained (in mol m^{-3}): $Ca(NO_3)_2$, 0.83; KNO_3, 0.43; $MgSO_4$, 0.33; KH_2PO_4, 0.57; $CaCl_2$, 0.17; micronutrients and Fe. NaCl (1 mol m^{-3}) was added to the medium on d 5, and was increased to 10 mol m^{-3} on d 6 with fresh growth solution. The growth solution was again replaced on d 10 and 12, and on d 12, the plants were randomized in new styrofoam islands for use in experiments on d 13. At this age, the plants were doubling in size every 2 d (the relative growth rate was 0.35 d^{-1}). The levels of K^+ and Na^+ in the growth medium were checked daily during the second week of growth by flame emission spectroscopy and were maintained with the required additions of KNO_3, NaCl and distilled water. Solutions were constantly aerated during all phases of the studies. Each experiment utilized at least 120 plants maintained in 8 L of growth solution until d 10, and in 12 L of solution thereafter. For the studies in Table I, salinity was increased on d 9, 10, and 11 to 50, 100, and 150 mol NaCl m^{-3} and plants were harvested on d 18. A ratio preceding MHS, such as 10:1 MHS, indicates the Na^+:K^+ concentrations in mol m^{-3}.

All studies were conducted in the walk-in growth chamber in which the plants were grown (13). The experiments were limited to 4 h (real time) in the middle of the photoperiod.

Experimental techniques were largely as described earlier for *S. marina* (12, 13). $^{22}Na^+$ and $^{42}K^+$ were used to double-label uptake solutions. Unless otherwise noted, uptake 'pulse' and chase solutions were identical to the growth solutions and were made from the same stock as that provided to the plants the evening prior to the experiment. Chase solutions were maintained free of label by using large volumes and replacing them frequently with fresh solution (13).

All counting, rinsing, harvesting, and data analyses were performed as previously reported (12, 13). As this lettuce has a root morphology (root diameter and branching pattern) similar to that of *S. marina*, the same protocol was used for rinsing the cell

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[3] Abbreviations: MHS, modified Hoagland solution; CHM, cycloheximide.

Table I. *Summary of Plant Fresh Weights and Ion Contents for Black-Seeded Simpson Lettuce Plants Grown at Different Levels of Salinity in Modified Hoagland Solution*

In all cases $[K^+]_{medium}$ was 1 mol m^{-3}. Plants were harvested 18 d after transfer to solution culture and at least 1 week after being salinized to the Na^+ level indicated. Data are means for 10 individual plants. Standard errors are less than 10% of the means in all cases.

Ions	$[Na^+]_{medium}$ (mol m^{-3})					
	0	1	10	50	100	150
	$\mu mol\ (g\ fr\ wt_{tissue})^{-1}$					
Plant fresh weight	5.4	5.1	5.8	5.0	3.4	2.0
$[Na^+]_{root}$	1.0	4.4	11	42	77	129
$[Na^+]_{shoot}$	0.9	7.5	35	82	151	248
$[K^+]_{root}$	80	86	73	56	62	50
$[K^+]_{shoot}$	76	76	51	27	25	34

wall. The sufficiency and completeness of the rinse was checked by comparing apparent uptake, in preliminary experiments, to that following an additional 10 min of rinse. Those studies confirmed that there was no leakage from internal compartments during the rinse, and that the removal of label from the wall was complete. As before, the root:shoot interfaces (about 3 mm) were assayed, but their contents are not included in our analyses since they never contained a critical portion of isotope. Lettuce does not appear to sequester Na^+ in this region.

In the final set of experiments, the effects of cycloheximide (CHM) were considered. CHM (20 $\mu g\ mL^{-1}$) was added to the double labeled uptake solution either during the final 8 min of a 20 min uptake period, or for the entire 20 min. To consider effects and differences associated with ion specificity rather than with concentration, these experiments were performed using 1:1 MHS, rather than the 10:1 MHS steady state medium.

RESULTS

Lettuce is a moderately salt sensitive crop species and growth reductions and necrosis are easily induced at salinities in excess of 100 mol NaCl m^{-3}. The variety used in these studies (Black-seeded Simpson) showed, however, a slight stimulation in growth in 10:1 MHS when compared to plants grown in Na^+-free (0:1 MHS), or 1:1 MHS (Table I). Growth was reduced and tissue Na^+ contents increased markedly at growth medium salinities of 50 mol NaCl m^{-3} and above. Shoot growth was reduced significantly more than root growth at those salinities, and root:shoot ratios increased from 0.3 to 0.4 by harvest.

Table I also indicates that Na^+ was not excluded from the shoot, even at very low salinities, nor was it accumulated in the root:shoot interface where the concentrations were similar to those in the roots. Root K^+ levels were relatively insensitive to Na^+, at least up to growth reducing salinities; shoot K^+ decreased considerably at the higher salinities.

We concluded, therefore, that, with 10:1 MHS grown plants, we could study the transport, compartmentation, and distribution of Na^+ and K^+ without studying unhealthy plants, but with substantial Na^+ accumulation. Further, we could expect those studies to provide results suitable for quantitative and qualitative comparisons to our earlier studies of *S. marina*.

The time courses of uptake and translocation of $^{22}Na^+$ and $^{42}K^+$ are shown in Figure 1. Data are presented only for the first 40 min so that the early points will be clearly visible; linearity was maintained in all cases through the 2 h duration of the studies. The most obvious difference between these results and those shown previously for *S. marina* (12, 13) was the low rate of root accumulation of $^{22}Na^+$. Otherwise, the results for the two species were similar—$^{22}Na^+$ translocation began within a few minutes; translocation of $^{42}K^+$ proceeded after a somewhat longer lag. Once established, however, both rates were constant with time.

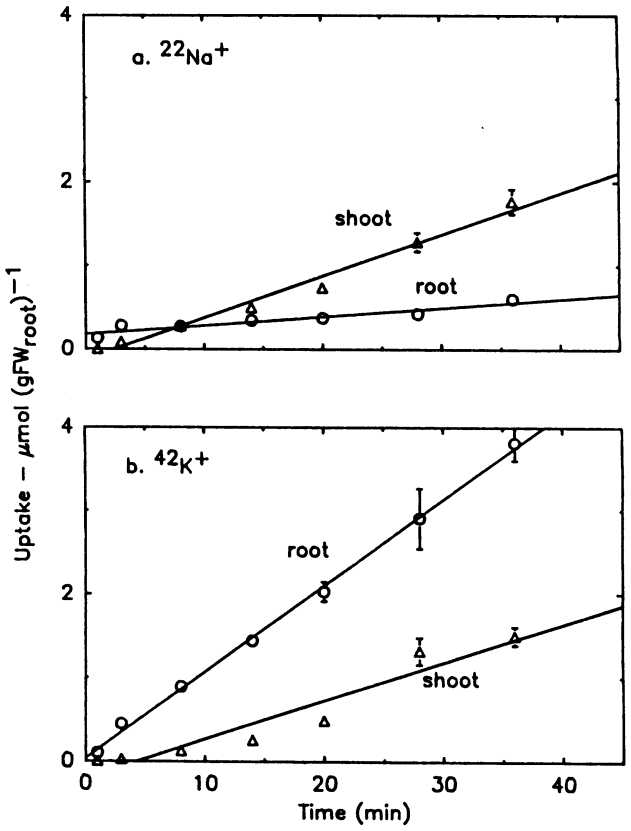

FIG. 1. Root accumulation (○) and translocation to the shoot (△) of $^{22}Na^+$ (a) and $^{42}K^+$ (b) in intact lettuce. Plants were grown in 10:1 MHS and the experiment was conducted at steady state. Linear regression and data are shown only for the first 40 min of a 120 min experiment for greatest visibility of early characteristics. For shoot data, only the nonzero values were included in the regressions. In all cases, linearity was maintained to 120 min. Data are means ± SE for each time point. Error bars smaller than symbols are not shown. Estimates of critical parameters are summarized in Table II.

Table II. *Summary of the Critical Parameters for the Experiments Shown in Figure 1*

The values are estimates of regression parameters (±SE) from first degree polynomial regressions, using the first 40 min for root accumulation and the entire 120 min time course for transport to the shoot.

Parameter	Units	Isotope	
		Na^+	K^+
α	$\mu mol\ (g\ fr\ wt_{root})^{-1}$	0.24 ± 0.02	0.52 ± 0.20
β	$\mu mol\ (g\ fr\ wt_{root})^{-1}\ h^{-1}$	0.43 ± 0.02	4.9 ± 0.2
γ	min	2.3 ± 1.5	8.3 ± 2.4
δ	$\mu mol\ (g\ fr\ wt_{root})^{-1}\ h^{-1}$	3.05 ± 0.06	4.4 ± 0.2

From plots such as those in Figure 1, we have previously identified several useful transport parameters (12), and these are summarized for lettuce in Table II. The extrapolation of the root accumulation line to time zero, α, is indicative of the contents of a rapidly exchanging root compartment; the x-intercept of the shoot accumulation line, γ, gives a first estimate of the time required for the translocating compartment to acquire label and pass it to the shoot; the slopes of the lines estimate the steady state rates of accumulation, β, and translocation, δ. Of particular

interest, in the absence of longer term net accumulation and partitioning data, was the ratio of the estimated translocation rates (0.70). This was close to the ratio of total Na^+:K^+ in the shoot (0.68; Table I) suggesting that these rates were equivalent to the growth-related ion fluxes to the shoot.

A rapidly established, constant rate of isotope transport to the shoot is possible only if the transporting compartments rapidly attain nonnegligible and constant specific activities. Thus, the total isotope accumulation rates (β plus δ, Table II) must underestimate the actual unidirectional influx rates (12). Figure 2a shows an alternative analysis for $^{22}Na^+$ based upon the assumption of an exponential decay of the apparent whole plant accumulation rate from a true unidirectional value toward a constant level which includes significant isotopic exchange. Unidirectional influxes (φ) and turnover rates of the initially labeled compartments were estimated from the extrapolation to time zero and decay half-times respectively (Fig. 2, *cf.* 12). As was the case for *S. marina* (13), accumulation of $^{42}K^+$ in very short times under steady state conditions was insufficient to allow similar analysis. However, if the external Na^+ and K^+ concentrations were reversed for the labeling period (*i.e.* 1:10 MHS, Fig. 2b), the results for K^+ were similar to those for Na^+.

The accumulation of label within the shoots under steady state conditions was analyzed similarly, providing a second estimate of the turnover rate of the compartment responsible for transport to the shoot (Fig. 3). This is equivalent to estimating the approach of translocation to linearity in Figure 1, and for Na^+ and K^+

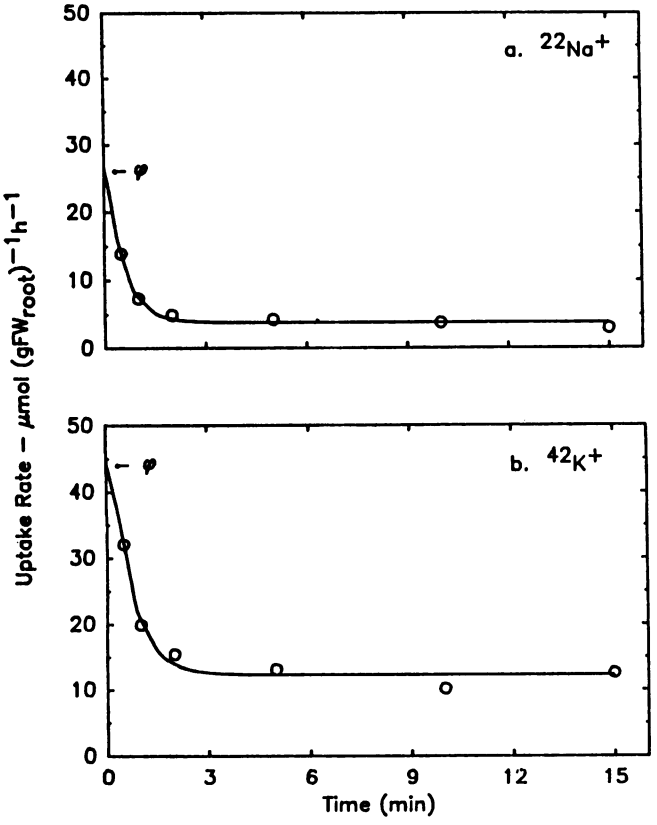

FIG. 2. Average total influx rates for $^{22}Na^+$ and $^{42}K^+$ in intact lettuce plants over the course of a 120 min labeling period. Rates were calculated for each sample by dividing total label in the plant by time of labeling. Curves were fit by nonlinear regression to a three parameter exponential decay model describing the decrease to a constant value. a, $^{22}Na^+$—steady state conditions (10:1 MHS); initial influx (φ) = 26 μmol $(gfr_{root})^{-1}h^{-1}$; $t_{1/2}$ = 0.35 min. b, $^{42}K^+$—labeling solution, 1:10 MHS; φ = 46 μmol $(gfr_{root})^{-1}h^{-1}$; $t_{1/2}$ = 0.42 min.

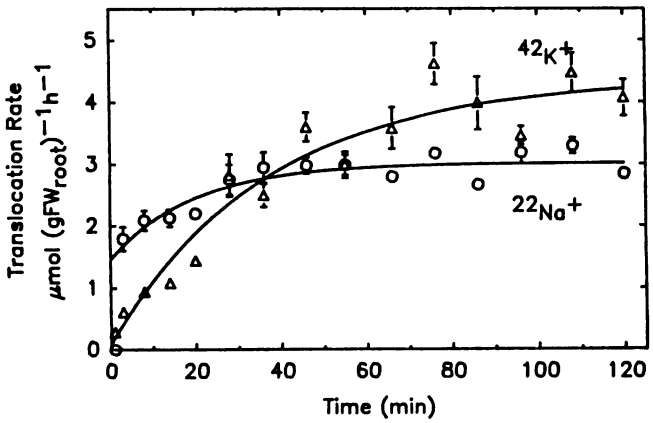

FIG. 3. Time dependence of translocation rate for $^{22}Na^+$ (O) and $^{42}K^+$ (Δ) in 120 min uptake experiments using lettuce under steady state conditions (1:10 MHS). Rates were calculated as the total label in each shoot sample divided by its time of harvest. The curves were fit by nonlinear derivative-free regression to a three parameter exponential decay model describing the increase to a constant rate. Data are means ± SE for each time point. Error bars smaller than the symbols are not shown.

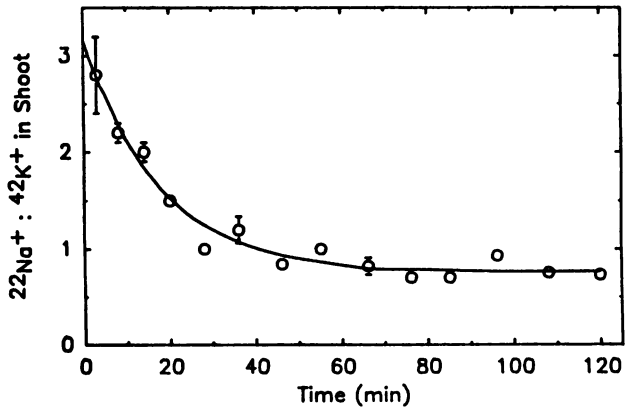

FIG. 4. The ratio of $^{22}Na^+$ to $^{42}K^+$ in the shoot of intact lettuce plants under steady state conditions over the course of a 120 min labeling period. The curve was fit by nonlinear derivative-free regression to a three parameter exponential decay model describing the decrease to a constant value. Data are means ± SE for each time point. Error bars smaller than the symbols are not shown.

respectively, the half-times were 13 (±3) and 26 (±4) min. For Na^+, this value must be an over-estimate, however; even though these curves show the best fit exponential approaches to a constant value, the actual curves for Na^+ as well as K^+ should pass through the origin.

Because the lag for $^{22}Na^+$ translocation was so short, a third estimate of the turnover rate of the K^+ translocating compartment could be made by plotting the ratio of the two isotopes in the shoot over time (Fig. 4). Assuming the rate of $^{22}Na^+$ translocation to be constant over the entire period, the half-time of the K^+ conducting component was estimated as 12 ± 2 min based upon the decay rate of the curve in Figure 4.

The relationship between the initially labeled compartments and those responsible for delivery of isotopes to the xylem was considered using pulse-chase studies. Figure 5 shows the transport of labels to the shoot during a 60 min chase following a 10 min pulse under steady state, 10:1 MHS growth conditions. As in *S. marina* under steady state conditions (13), the total $^{42}K^+$ content of the plants did not decrease during the chase. Rapid loss of $^{22}Na^+$ did occur, however, again as previously reported, and the amount of that loss was approximately the same as the

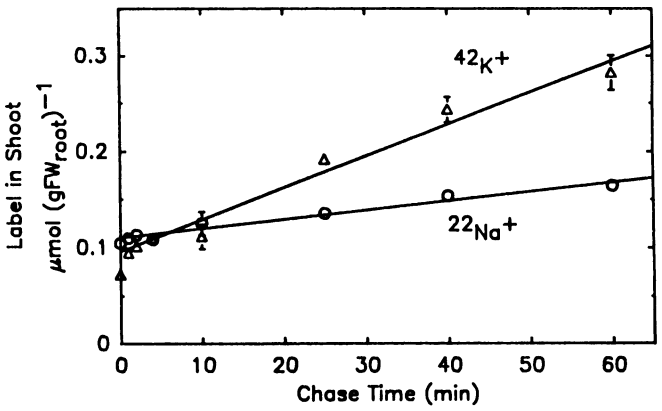

FIG. 5. Chase period translocation of $^{22}Na^+$ (O) and $^{42}K^+$ (Δ) in intact lettuce plants under steady state conditions (10:1 MHS). Lines were fit by linear regression to the data for the 4 to 60 min period to avoid overestimations of rates. Data are means ± SE for each time point. Error bars smaller than the symbols are not shown.

Table III. *Effects of Cycloheximide (20 μg ml^{-1}) on Root Accumulation and Transport to the Shoot of $^{22}Na^+$ and $^{42}K^+$ in Lettuce*

Plants were grown in 10:1 MHS and transferred to 1:1 MHS at the beginning of the labeling period. CHM treatments were for the entire 20 min labeling period, or for the last 8 min only. For all data, standard errors were less than 5% of the means. Control rates were averaged over the 20 min labeling period.

Growth	Control	Treatment	
		CHM, 8 min	CHM, 20 min
	μmol (g fr wt$_{root}$)$^{-1}$ h^{-1}	*% of control*	
$^{22}Na^+$			
root	0.13	176	550
shoot	0.23	100	79
total	0.36	127	247
$^{42}K^+$			
root	5.6	74	57
shoot	1.0	72	43
total	6.6	74	54

rapid uptake to the roots indicated in Figure 1 and Table II (data not shown).

Following the first few minutes of the chase, there was little, if any, further transport of $^{22}Na^+$ to the shoot. $^{42}K^+$ translocation continued, however, throughout the chase, and after 60 min, shoot $^{42}K^+$ contents were three times those at the end of the pulse. Under nonsteady state conditions (1:10 MHS for pulse and chase) similar continued translocation of $^{42}K^+$ occurred, but it was accompanied by a small, rapid loss of label from the plants as a whole (data not shown). Again, the results are similar to those reported for *S. marina* (13).

These results suggested a difference in the transport pathways for the two ions, and that there was little direct exchange between the K^+ translocating symplasm and the medium. We explored these possibilities further with chemical modifiers hoping to differentially alter the uptake and partitioning of the ions. Effects of this sort have been reported in a number of other systems using a number of chemicals, including amino acid analogs, transport inhibitors, abscisic acid, and CHM (11, 19, 22, 26). In preliminary studies, the latter produced the largest and most rapid effects, and therefore was chosen for more detailed experiments.

The effects of CHM were considered in 20 min isotope uptake studies, and the results are summarized in Table III. CHM (20 μg ml^{-1}) was added either at the start of the 20 min labeling period, or, to indicate the rapidity with which the modifier effects could be measured, for the final 8 min only. In order to consider qualitative differences in the systems for transport and partitioning of the ions and to emphasize effects associated with specificity rather than with concentration, the plants in these experiments were transferred to 1:1 MHS at the beginning of the labeling period.

Table IV. *Effects of Cycloheximide (20 μg ml^{-1}) on $^{22}Na^+$ Transport in Pulse Chase Studies Using Intact Lettuce Plants*

Plants were grown in 10:1 MHS and transferred to 1:1 MHS at the beginning of the labeling period. CHM was present in treated plants for the entire pulse. Plants were labeled for 20 min and chased for 40 min. Δ represents the change in label contents during the chase period. Data are means of six samples. Standard errors were less than 10% in all cases.

Growth	Contents		
	Root	Shoot	Total
		μmol (g fr wt$_{root}$)$^{-1}$	
Control			
20 min pulse	0.042	0.076	0.118
+40 min chase	0.013	0.080	0.093
Δ	−0.029	0.004	−0.025
+CHM			
20 min pulse	0.233	0.060	0.293
+40 min chase	0.148	0.131	0.279
Δ	−0.085	0.071	−0.014

CHM altered both total uptake and isotope partitioning between roots and shoots, and based on the results with plants treated only for the last 8 min of the experiment, the effects were rapid. (These results do not reflect changes in transpiration which was unaltered for at least 60 min of CHM treatment.) The effects were different for the two ions. Total $^{22}Na^+$ accumulation was increased, reflecting a much larger effect on root accumulation; transport to the shoot was reduced more than 20% over the 20 min period. As a result, while about 65% of all the Na^+ label was in the shoot after 20 min in the control plants, only 20% was transported in the CHM treated plants. For $^{42}K^+$, transport to the shoot was also reduced, but only to about the extent that overall accumulation within the plants was altered. At the end of 20 min, 15 and 12% of the label was in the shoots of control and plants treated for 20 min, respectively.

Finally, CHM also changed the unloading characteristics of the Na^+ symplast (Table IV). When plants were pulsed for 20 min with $^{22}Na^+$ in the absence of CHM, then chased for 40 min, partitioning of label lost from the roots was similar to that previously reported in pulse chase studies using *S. marina*; only 14% of the lost label moved to the shoot. With CHM treatment, 85% of the label leaving the roots moved to the shoots.

DISCUSSION

In this report, we have used the techniques developed in our studies of *S. marina* to consider the transport of Na^+ and K^+ in lettuce. As in the halophyte studies, we have used intact plants growing at steady state on a complete nutrient medium. Though lettuce is a moderately salt sensitive mesophyte, we have avoided the question of 'salt tolerance' *per se*; the level of salt involved was sufficient to produce appreciable accumulation of Na^+ in both the roots and shoots, but not to reduce growth. Thus, in the case of Na^+, our objective was to characterize transport associated with the successful management of a potentially toxic ion. The study of K^+, as well, provided physiologically interesting and significant characteristics for purposes of comparison both to Na^+ and to other transport studies.

In all aspects, the present results were qualitatively similar to those reported for *S. marina*. First, for both ions, transport to

the shoot began within minutes of the start of labeling, and accounted for a significant portion of the total accumulation. Accumulation of K^+ in the root exceeded transport to the shoot for at least 2 h. For Na^+, more than half the total label was in the shoot after 8 min (Fig. 1a), and the rates of translocation were similar to those in the halophyte. Under steady state conditions in 10:1 MHS medium, $^{22}Na^+$ translocation was nearly 25% of the rate reported for *S. marina* in 90:2 modified sea water and 250% of the rate in 1:1 modified sea water. In contrast, the roots accounted for only 12% of the total Na^+ accumulation in lettuce (Table II), and for 25 and 48% in *S. marina* at moderate and low salinities, respectively (12, 13).

Second, the accumulation of $^{22}Na^+$ was initially very fast, indicating the presence of a small, rapidly exchanging compartment. The turnover time for the compartment was less than 30 s (Fig. 2), again comparable to that reported for the halophyte (12, 13). At elevated uptake medium levels, a similar result was found for K^+. For both ions, the content of the compartment involved was only about 2% of the total root contents, and was directly proportional to the external concentration (data not shown).

Third, a small compartment was implicated in the delivery of Na^+ to the shoot. Rapid turnover of the transporting compartment was indicated both by the rapid appearance of label in the shoot and by the failure of nonlinear regression procedures to fit a curve for the rate of translocation which passed through the origin (Fig. 3). In pulse-chase studies, Na^+ translocation stopped almost immediately once label was no longer available for uptake. Label was lost as quickly to the medium, in an amount comparable to that indicated for the contents of the small compartment.

Fourth, at least at physiologically relevant concentrations, a separate system was indicated for accumulation and transport of K^+. Based upon the time required for translocation to begin (Fig. 1), and on two methods of estimating the time required to establish a constant translocation rate (Figs. 3 and 4), the turnover time of the K^+ conducting compartment was two to four times longer than that for Na^+. The labeling of this compartment was not by exchange with the medium or with other compartments in the roots. In pulse-chase studies, translocation continued after labeling at an apparently constant rate for at least 60 min.

These results indicate that those previously reported for the halophyte system were not a peculiarity of the species nor of its tolerant nature, but rather were characteristics made apparent by the experimental and analytical methods. They also support the conclusion that the systems involved in transport of Na^+ and K^+ are distinct and separately controlled; Na^+ accumulation in mesophytes is not the result of competition between Na^+ and K^+ for one set of transporters, or of the failure of K^+ transporters to discriminate efficiently against Na^+ (2). And, they support at least some of the well established dogma based on 'simple' systems. The K^+ results indicate rapid, unidirectional accumulation from the external medium, and are consistent with the hypothesis that initial K^+ accumulation involves a specific uniporter at the epidermal plasma membrane.

On the other hand, as K^+ exchange with the medium was not found under physiological conditions, the data do not support the traditional 'bulk cytoplasm' and vacuole model of the root, with the continuous, and exchangeable cytoplasm delivering ions back to the medium, to the root cell vacuoles, and to the xylem. Other investigators have also commented on difficulties in the concept of a single compartment feeding the vacuole and the xylem (10, 17), and more recently, in studies of nitrate transport, the delivery of unreduced NO_3^- across a root having a substantial nitrate reductase activity led Rufty *et al.* (20) to postulate a specialized transporting compartment in corn roots.

For Na^+ transport, the physical identity of the small, symplastic compartment and the mechanism by which its contents turn over are central questions for future studies, particularly with regard to the role of Na^+ in salinity tolerance. Based on a number of precedents in the literature, we have suggested that the uptake system itself might involve endocytosis (8, 14, 16, 18), and that the small, transporting symplasm might be the ER (1, 15, 25). In the final experimental section of this report, we have explored the possibility of altering the various Na^+ transport systems differentially, settling on the use of CHM for detailed studies. Even with very brief treatments, the effects on transport were large and complex, arguing against an effect mediated through protein synthesis. In this regard, it is interesting that earlier experiments on the effects of CHM on transport across barley roots were also interpreted as indicating involvement of vesicles (11).

It remains to be seen what form of a vesicular explanation is reasonable, and to what extent the involvement of general membrane circulation (24), more sophisticated Na^+ receptors, or transporters might be required. The simple hypothesis that uptake involves passive inclusion of ions within endocytotic vesicles is undoubtedly not reasonable (7, 21). Even though external levels of Na^+ can be much higher than those of other nutrients, for a rate of 400 μmol Na^+ (g fr wt_{root})$^{-1}h^{-1}$ from a 90 mM NaCl solution, the entire volume equivalent of the root would need to turn over every 15 min. Because of the high surface-to-volume ratio of endocytotic vesicles, however, the turnover of cell volume is slow (about 80 h) even when the cell surface turnover is fast (*i.e.* 10 min) (21).

With this series of studies, however, we have established a methodology for the analysis of ion transport in intact, fully autotrophic plants, we have shown it to be applicable to two species whose responses to salinity are very different, and we have identified enough salient features of the Na^+ transport system to move toward a more detailed analysis at the biochemical level. The results of those studies will be presented in subsequent reports.

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