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Sodium and Potassium Compartmentation and Transport across the Roots of Intact *Spergularia marina*[1]

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ABSTRACT

The Na^+ and K^+ transport characteristics of *Spergularia marina* (L.) Griseb. were considered in order to compare the systems by which these two physiologically different cations are managed during initial acquisition and subsequent partitioning in midvegetative plants. Uptake of $^{22}Na^+$ and $^{42}K^+$ and redistribution of labels in pulse-chase studies were compared under steady state growth conditions or with the concentration of one of the ions elevated. At high external concentrations, the initial $^{42}K^+$ accumulation and transport to the shoot was associated with a small, rapidly exchanging, cellular compartment similar to that previously indicated for Na^+ (D Lazof, JM Cheeseman 1986 Plant Physiol 81: 742–747). At 1 mol m^{-3}, K^+ was conducted to the shoot through a root compartment, the specific activity of which rose much more slowly than the rapidly exchanging compartment. After a lag of approximately 5 minutes, $^{42}K^+$ translocation approached a constant rate with a half-time of 14 minutes compared to 5 minutes for $^{22}Na^+$ or for $^{42}K^+$ at higher external levels. At all external levels, prolonged translocation of $^{42}K^+$ was measured when a 10 minute pulse was followed by an unlabeled chase, again suggesting a conducting compartment distinct from that for Na^+. It is suggested that the K^+ conducting compartment, possibly the 'bulk cytoplasm,' is associated with the active K^+ transport system generally found in higher plants.

The partitioning of mineral resources between the above and below ground parts of a plant is controlled by the root. It is largely mediated through transmembrane events, with a negligible contribution of apoplastic movements (11, 17). The systems responsible for providing a controlled nutrient supply to a rapidly growing shoot and maintaining the ion levels in the root itself, however, are still not well understood. Despite the desirability of 'simple' systems for transport studies, nutrient management is better considered within the complexity of an intact growing plant.

Among the difficulties facing organismal transport studies is interpretation of isotope flux studies when unidirectional fluxes cannot be measured. In a previous report (16), we addressed these problems, considering the transport and accumulation of labeled Na^+ in *Spergularia marina* growing at moderate salinity. Using the approach of integrated pulse-chase protocols, transport events related to an internal root compartment other than 'bulk cytoplasm' and 'vacuole' were distinguished.

Even in a halophyte, Na^+ may well be a special case, particularly when the external concentrations to which the plants are exposed are high, both absolutely and relative to other cations. In this report, therefore, we extend our studies to lower salinity conditions and to K^+. Our objective is to consider Na^+ and K^+ transport under comparable conditions, with particular concern for the mechanisms of initial acquisition, for compartmentation within the roots, and for delivery of the ions to the xylem.

MATERIALS AND METHODS

Spergularia marina (L.) Griseb. seeds were collected from plants growing in growth chambers, germinated, and transferred to solution culture and grown as described previously (8, 9). Briefly, plants were selected for uniformity and were transferred to solution culture approximately 2 weeks after germination; all ages will refer to days after transplanting. The initial growth medium was Na^+-free, 0.1 × MSW[3] containing (in mol m^{-3}): KNO_3, 0.75; $KHCO_3$, 0.265; $CaCl_2$, 1.05; $MgSO_4$, 3.2; $MgCl_2$, 2.3; $(NH_4)H_2PO_4$, 0.5; micronutrients and Fe.

On d 7, 1 mol m^{-3} NaCl was added to the medium. This solution is designated 1:1 MSW. In all cases, experimental solutions are identified by the concentration ratio of Na^+ to K^+, with concentrations given in mol m^{-3}; MSW is otherwise identical in all experimental and growth solutions. Growth solutions were assayed and adjusted for Na^+ and K^+ daily using NO_3^- salts, and fresh solution was provided on d 7, 14, and 16.

All experiments utilized plants 17 d after transplanting. The plants were grown and the experiments performed in the same growth chamber. The chamber had a 15 h photoperiod and a day/night temperature regime of 25°C/16°C. Irradiance was 350 to 450 μmol m^{-2} s^{-1} provided by F96T12/D/SHO fluorescent tubes approximately 1.5 m above plant height. Chamber relative humidity was uncontrolled and varied considerably over the period of these studies, though within any one experiment it was constant. The lack of a humidity or transpiration effect on K^+ and Na^+ uptake and partitioning has been reported in a previous paper (6). Solutions were aerated during all phases of the study.

For isotope studies, uptake media were double labeled with $^{22}Na^+$ and $^{42}K^+$. The $^{22}Na^+$ was obtained from New England Nuclear; $^{42}K^+$ was prepared locally by irradiation of K_2CO_3 in the central thimble of the TRIGA reactor, University of Illinois Nuclear Engineering Program. Samples of $^{42}K^+$ were neutralized with H_2SO_4 following irradiation. The specific activity of the labeled solutions differed among experiments and depended in part upon the labeling protocols and expected uptake rates.

Plants were randomized in styrofoam islands as they were set into fresh solution on d 16. These islands were designed according to the replicate and sampling needs of each experiment. The plants remained in the islands until they were submerged into the first $CaCl_2$ rinse upon harvest. Plants were moved through a series of three ice-cold $CaCl_2$ rinses (20 mol m^{-3}) with a total

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[3] Abbreviation: MSW, modified sea water.

rinse volume of 10 L. Total rinse time was 3.5 min. The sufficiency of this rinsing procedure to remove all label from the cell wall, while preventing any loss from membrane-bound compartments was discussed previously (8, 16).

Plants were individually harvested directly from the final rinse into gamma counting vials. The shoots and root:shoot interfaces were immediately severed from the roots. The interfaces (about 2 mm) were assayed, but were not included in subsequent analyses since they never contained more than 5% of the total counts of either isotope. All counting was done with an LKB 1282 Compugamma counter. In order to maintain extremely low counting errors, samples were counted with a single wide-open window and recounted after complete decay of $^{42}K^+$. Decay corrections and isotope contents were calculated following the second counting. Each sample consisted of the roots or shoot of a single plant. All weights were obtained dry on a Cahn microbalance to three significant digits. Conversion to fresh weight was based on average moisture contents of 92.8 and 91.6 ± 0.1% for roots and shoots, respectively (16).

In the figures, each point represents the mean of at least eight plants, and each figure presents the data from a single representative experiment; all protocols were used in at least three separate studies. Statistical analyses were performed using the BMDP Statistical Software Package (10).

Short time-course studies measuring low levels of isotope transport required extra precautions against contamination or loss of sample; the careful rinsing and the direct harvest into the counting vials without blotting the plant sample minimized those errors. In pulse-chase studies, large quantities of chase solutions were used so that plants would not acquire label from the solution during the chase. Samples were passed through a series of chase solutions changed at intervals to maintain them free of tracer. Contamination of the chase solution was checked, both by counting several milliliters of the chase solution, and by setting islands of nonpulsed plants directly into the 'used' chase solution for an hour. There was no labeling of plants during this period.

The final set of experiments considered acquisition of K^+ from low concentration solutions. Two treatments were used; half the plants were transferred to 1:0.1 MSW 4 min prior to labeling (to avoid K^+ carry-over to the pulse solution), and half were maintained in 1:0.1 MSW for 24 h preceding the experiment. The K^+ level was monitored by flame emission spectrophotometry (IL643, Instrumentation Laboratory Inc; Lexingtgon, MA) using the prediluted mode with redissolved oven-dried solution samples. The solution K^+ concentration was between 120 and 90 mmol m^{-3} K^+ during the pretreatment.

RESULTS

An inherent feature of isotope tracer studies of membrane transport is that straightforward estimation of undirectional movements is possible only so long as the specific activity of an initially unlabeled region remains negligible, or so long as movement in the opposite direction does not occur. We have previously shown that, for *S. marina* growing at moderate salinity, this period is less than 1 min for fluxes of $^{22}Na^+$ (16). Details of the methods allowing interpretation of isotope-flux results under these more demanding conditions were given in that report. In experiments lasting beyond 1 min, isotope accumulation rates declined exponentially with time. Unidirectional influx rates were estimated by analysis of the approach of the rate to a constant value (16).

Comparable kinetics were observed for both $^{22}Na^+$ and $^{42}K^+$ when plants grown on 1:1 MSW were transferred to 25 mol m^{-3} solution for uptake measurements. Figure 1 shows analysis of $^{42}K^+$ uptake rates from 1:25 MSW (Na^+ was maintained at 1 mol m^{-3}). The y-intercept, φ, is an estimate of the unidirectional influx rate (16). The turnover rate of the compartment involved in these initial fluxes is estimated by the decay time constant of the apparent uptake rate. Total contents of the compartment can be estimated by integration of the area under the decay portion of the curves, though a simpler method is extrapolation to time zero of a linear regression of total label *versus* time (α; see inset, Fig. 1). Results similar to those in Figure 1 were obtained for $^{22}Na^+$ in 25:1 MSW (Na^+ concentration elevated; K^+ maintained at 1 mol m^{-3}). Uptake rates, turnover rates, and compartmental contents for both Na^+ and K^+ are summarized in Table I.

As in our previous report for steady state experiments performed with *S. marina* grown in 90:2 MSW (16), the linear rate of $^{22}Na^+$ translocation to the shoot during a pulse in 25:1 MSW was established within 2 min (data not shown). Also as previously reported, an amount of $^{22}Na^+$ equal to that in the rapidly exchanging compartment was lost from the roots upon transfer to unlabeled medium (data not shown). This loss was largely to the medium and was complete within a few minutes. Additional translocation to the shoot during this period accounted for only about 10% of the total loss from the roots.

The kinetics of $^{42}K^+$ translocation and exchange transport following a 10 min pulse in 1:25 MSW are shown in Figure 2. At this level of external K^+, there was a small, rapid loss of label to the chase medium (inset, Fig. 2). This loss was similar to that found for $^{22}Na^+$, but while chase-period $^{22}Na^+$ translocation was nil after 2 min (*cf* REf. 16), translocation of $^{42}K^+$ continued for at least 16 min at 83% of the rate averaged during the pulse.

The conditions used for the K^+ studies in Figures 1 and 2 were selected in order to consider whether K^+ might be transported by the systems previously suggested for Na^+ (16). Preliminary studies indicated that the rapidly exchanging component and the high initial fluxes (Figs. 1 and 2 and Ref. 16) were difficult to measure, if not absent, in 1:1 MSW; therefore, an elevated concentration was used during labeling. Further detailed studies were conducted under steady state growth conditions.

The results of a time-course of uptake experiment for *S. marina* plants in 1:1 MSW are shown in Figure 3. Extrapolating total uptake to time zero gave a value not significantly different from zero for either ion (compare to inset, Fig. 1). This was expected based upon our previous observation that the contents of the rapidly exchanging Na^+ compartment were proportional to the external ion concentration (16). Although translocation of both isotopes to the shoot began after a short lag, Figure 3 indicates that a linear relationship was established more quickly for $^{22}Na^+$. Though a curve was fit in Figure 3b to emphasize the slower rise of K^+ translocation, a constant rate was established after 20 to 30 min in these studies (*cf.* Ref. 8). Assuming an exponential approach to a constant translocation rate, *i.e.* using the same analytical methods as were applied to the data in Figure 1 but substituting the rate of translocation for the rate of total influx, the data in Figure 3 were used to estimate the rate of turnover of the translocating root compartment. After a lag of 2 min, the linear translocation rate for Na^+ was established with a half-time of 4.90 ± 0.5 min. The corresponding half-time for K^+ was estimated at 14 ± 2 min.

This steady state rate of turnover for the K^+ conducting symplasm suggested that translocation during a chase might continue for much longer than the 16 min indicated in Figure 2. Results of pulse-chase experiments at the 1:1 MSW steady state were qualitatively similar to those reported above. Upward movement of $^{22}Na^+$ ceased immediately after plants were transferred to unlabeled solution. Translocation of $^{42}K^+$ appeared constant, however, through a chase period of 60 min (Fig. 4), though the rate was a somewhat smaller fraction of the averaged translocation rate during the preceding 10 min pulse (20%) than was found for the elevated K^+ experiments in Figure 2.

Finally, the transport characteristics for K^+ in *S. marina* were considered under conditions more comparable to those used in

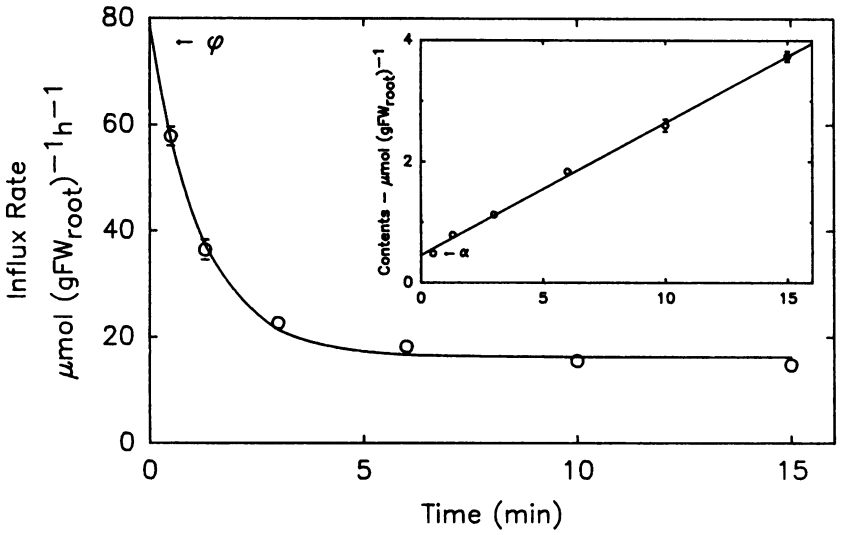

FIG. 1. Influx rate for $^{42}K^+$ into intact *S. marina* plants *versus* time in labeled solution. Plants grown in 1:1 MSW were transferred to 1:25 MSW for the labeling. Average uptake rates were calculated as total uptake in an experimental period divided by total elapsed time in labeled solution. Curves were fit by derivative-free, nonlinear regression analysis to a three parameter exponential model describing decay to a constant value. φ estimates the unidirectional influx rate. Data are means ± SE for each time point; n = 8. Error bars smaller than symbols are not shown. Inset: total label in the plant *versus* time in labeled solution. α estimates the contents of the most rapidly exchanging compartment.

Table I. *Summary of Isotope Flux Characteristics for K^+ and Na^+ in Intact S. marina Plants*

Plants grown in 1:1 MSW were transferred to 1:25 MSW or 25:1 MSW for labeling with $^{42}K^+$ or $^{22}Na^+$, respectively. Unidirectional and steady state influx rates and turnover rates of the initially labeled compartment were determined by derivative-free, nonlinear regression (see Fig. 1). Errors are asymptotic standard deviations. The contents of the rapidly exchanging, initially labeled compartment were estimated as the extrapolation to time zero of the linear regression of total label in the plant (α in Fig. 1). K^+ data are those presented graphically in Figure 1.

Ion	Influx Rate		Turnover Rate	Compartment Contents
	Unidirectional	Steady state		
	μmol (g fr wt$_{root}$)$^{-1}$ h^{-1}		*min*	*μmol (g fr wt$_{root}$)$^{-1}$*
K^+	79 ± 4	16.1 ± 0.7	0.7 ± 0.2	0.55 ± 0.02
Na^+	47 ± 4	10.6 ± 0.8	0.8 ± 0.4	0.34 ± 0.02

studies of mesophytes, with a pulse-chase experiment conducted at 1:0.1 MSW. Plants were either grown continuously in 1:1 MSW, or were transferred to low K^+ conditions (1:0.1 MSW) 24 h prior to the experiment. Root accumulation of $^{42}K^+$ was 60% greater for the pretreated plants over a 10 min uptake period (data not shown). K^+ translocation to the shoot during the pulse and the chase was also increased, though to a much lesser extent (Fig. 5). The results indicate that *S. marina* cultured under complete nutrient conditions has a well developed capacity to acquire K^+ and to deliver it to the shoot from an external medium low in K^+, but that the responsible systems can still be stimulated by low K^+ pretreatment.

In both treatments, the $^{42}K^+$ content of the shoots increased fourfold during the 40 min chase (Fig. 5). In the case of plants preexposed to low K^+ for 24 h, the rate of increase was more or less constant. This result is somewhat difficult to explain because the specific activity of any steady state conducting compartment must decrease with ongoing translocation, causing a decrease in the amount of label moving to the shoot over time. For the controls in Figure 5, that expectation was more nearly realized. We were not, however, able to fit a curve to those data which rose exponentially to a constant shoot content of $^{42}K^+$; rather than use either a polynomial or an 'eyeball' description without a mechanistic basis, therefore, a linear fit is shown to emphasize the nonlinearity.

DISCUSSION

In this report, we have compared the transport of K^+ and Na^+ by mid-vegetative *S. marina* plants growing in 1:1 MSW. As in our previous studies (16), we have used plants growing under steady state conditions in complete nutrient medium, our objec-

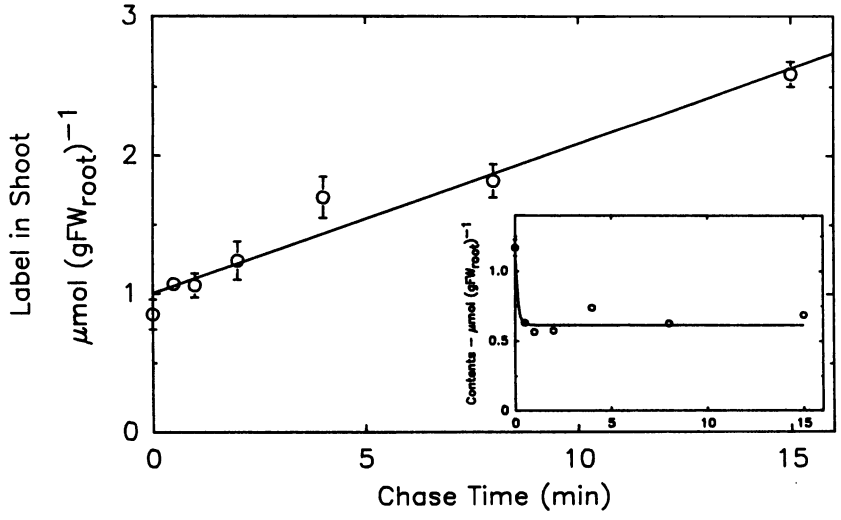

FIG. 2. $^{42}K^+$ translocation to the shoots of intact *S. marina* plants in a pulse-chase experiment. Following a 10 min pulse in labeled 1:25 MSW, plants were transferred to unlabeled medium and harvested at the times indicated. The line was placed by linear regression. Inset: loss of label to the external medium during the chase for the same experiment. The curve describes exponential decay to a constant level. Standard errors are shown when larger than symbols; n = 8.

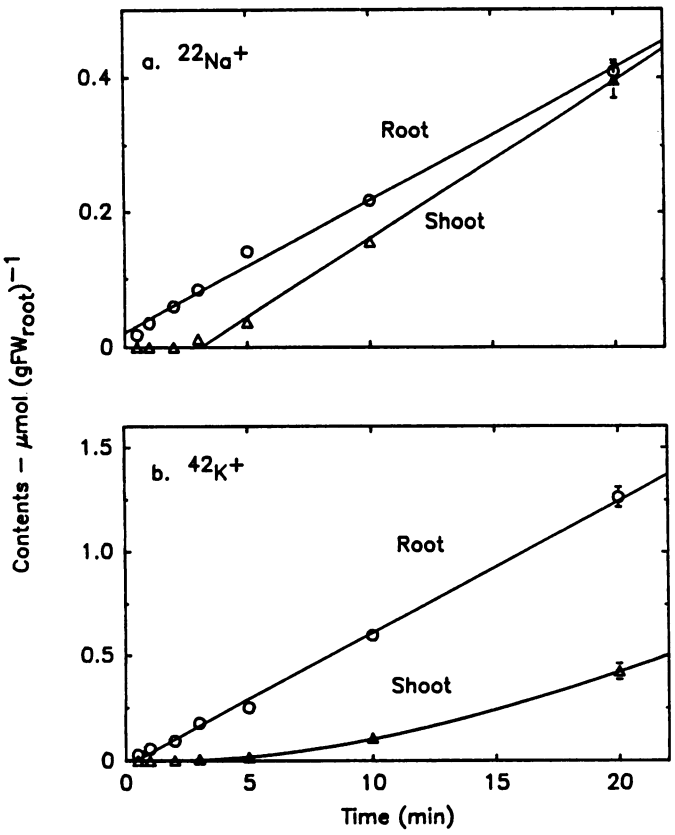

FIG. 3. Root accumulation and translocation to the shoot of $^{22}Na^+$ and $^{42}K^+$ in intact *S. marina*. Plants were grown in 1:1 MSW and labeled under steady state conditions. (a) Na^+, linear regression shown. For translocation to the shoot, only nonzero values were used in the analysis. (b) K^+, the root accumulation was fit by linear regression. For translocation to the shoot, a third order polynomial is shown in order to emphasize the slower rise to linearity for K^+ by comparison to Na^+.

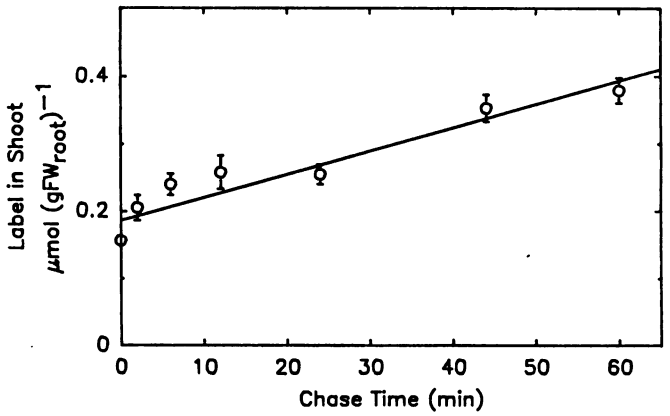

FIG. 4. Chase-period translocation of $^{42}K^+$ in intact *S. marina* under steady state conditions (1:1 MSW). Plants were transferred to unlabeled solution following a 10 min pulse. The linear regression was sufficient; higher degrees of polynomial did not statistically improve the multiple correlation coefficient.

tive being to characterize transport as it relates to ongoing plant nutrition.

A priori, differences in the results with the two ions were expected. Na^+ is potentially toxic and excluded against a substantial electrochemical gradient, even in halophytes such as *S. marina* (5, 8). K^+, on the other hand, is accumulated by most plants, even when available at low concentrations. At the same

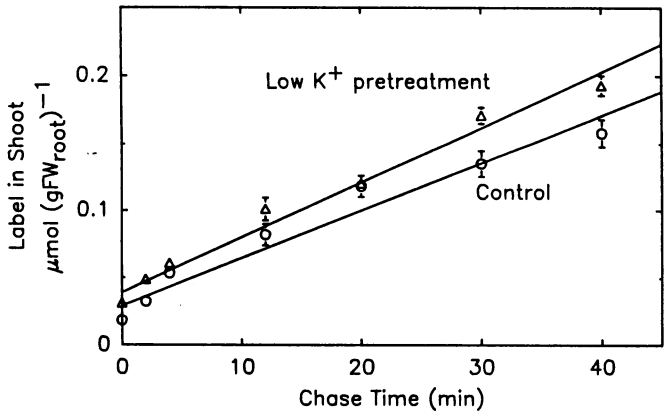

FIG. 5. Chase period translocation of $^{42}K^+$ in intact *S. marina* under conditions of reduced external K^+ concentration. Plants were transferred to unlabeled medium following a 10 min pulse. Control: plants grown in 1:1 MSW were transferred to 1:0.1 MSW just prior to labeling. Low K^+ pretreatment: plants were moved to 1:0.1 MSW 24 h prior to the experiment.

time, however, the long term, growth related accumulation of the ions in roots and shoots is very similar over a range of salinities at least up to 0.4 × seawater (180:4 MSW) (9).

It was not altogether surprising, therefore, that both similarities and differences were found. Overall, steady rates of accumulation were similar for $^{42}K^+$ and $^{22}Na^+$, while the approach to constant isotope flux and pulse-chase isotope exchange characteristics were different. We will return to the interpretation of these results shortly.

Superficially, there are a number of similarities between the present results and those reported, for example, by the Leiden group (1, 2, 12, 14). For barley seedlings previously deprived or depleted of one or more essential nutrients ('low-salt"), their studies emphasized the accumulation of Na^+ and K^+ as the plants were partially relieved of that stress. They have reported, for example, a rapid cessation of Na^+ transport to the shoot after its removal from the external medium that appears similar to that reported here (2, 12). K^+ transport, on the other hand, continued, and a 'special structure or organelle' involved in the transfer of K^+ to the xylem was hypothesized (13).

The striking difference between the barley and *S. marina* studies, was the time scale on which the events occurred, or at least, were considered. Though the time dependence of root accumulation and upward translocation of $^{86}Rb^+$ during pulses and chases (1) had a form similar to that shown here for $^{42}K^+$, in our studies the transport events were at least two orders of magnitude faster. Though barley might operate on a much slower time scale, it is more likely that these differences were determined by the experimental protocols. We have shown, for example, that Na^+ exchange in corn roots occurs on the same time scale as it does in *S. marina* (3), and that protocols which do not include very short time points cannot indicate, let alone resolve, such exchange (4).

We return, therefore, to the problem of interpreting and generalizing our studies with respect to the systems and compartmentation underlying the results. As we have previously noted, a constant rate of upward transport equivalent to that supporting shoot growth requires that the transporting compartment be at a specific activity equal to that of the uptake medium (16). Particularly in view of the rapidity with which such Na^+ transport was established, an apoplastic pathway controlled by transpiration and bypassing the endodermal control point could be suggested. We have shown, however, that neither transport to the shoot nor root accumulation is controlled by transpiration (6), consistent also with the conclusion of Pitman and Wellfare from studies of

hydraulic conductivity and ion transport across barley roots (18). Instead, we have concluded that the compartment which exchanges rapidly with the external medium is also responsible for delivery of Na^+ to the xylem, and we have echoed suggestions from a number of laboratories that the endoplasmic reticulum might be that compartment (16).

In this study, uptake of K^+ into a rapidly exchanging compartment was also demonstrated. The characteristics of this transport were similar to those for Na^+ at moderate salinity, but only at K^+ concentrations higher than those of full strength seawater; there was a high initial apparent $^{42}K^+$ influx (Fig. 1), a significant positive *y*-intercept of the linear regression of total influx *versus* time in uptake solution (inset, Fig. 1), and a rapid initial loss of $^{42}K^+$ from the roots to the medium during the early chase (inset, Fig. 2).

The major physiological pathway for K^+ entry, however, does not appear to be that involved in Na^+ transport, and as the final set of experiments with the low K^+ pretreatment show, the active, starvation-stimulated K^+ uptake system central to transport research for the last 50 years is present in *S. marina* (*cf.* 8). Clearly, it is the obvious choice as the normal mechanism for initial K^+ entry.

Beyond the initial uptake step, control of subsequent partitioning is most important to understanding organismal ion relations (5). For Na^+ at high or low salinities, the similar responses of root accumulation and transport to chemical modifiers supports the hypothesis of a common control for the overall fluxes at the point of entry to the roots (*cf.* 8, 16). Subsequent partitioning of label between the external solution, the more slowly exchanging root compartments and the shoot involves secondary movements. There is, however, specificity in those secondary movements; at 1 mol m^{-3}, the steady state Na^+ influx rate (Fig. 3a) was about 30% of the rate at 25 mol m^{-3} (Table I), much less reduced than the contents of the small symplastic compartment. Further, the roots retained a larger portion of the total label (compare Fig. 3a with Fig. 3, Ref. 16). Whether the differences of these movements reflect specificities within or between cell types (19) is as yet uncertain.

The inhibition of $^{42}K^+$ accumulation in the roots and transport to the shoots by DCCD and DNP was also similar, though both were more strongly reduced than Na^+ fluxes (8), again suggesting that a single mechanism might exert overall control on K^+ movements. On the other hand, the stimulation of root accumulation by fusicoccin was much greater than the stimulation of upward transport. Thus, for K^+ as well as Na^+, multiple secondary transport control points are likely.

More difficult to explain is the translocation of K^+ and its movement in the chase period of pulse-chase studies. At low external concentrations, the slower rise to the maximal rate of translocation (Fig. 3b), and prolonged movement of label to the shoot during the chase without measurable loss to the medium suggest that the upwardly mobile K^+ is in a compartment having a large total K^+ content. That compartment must not exchange appreciably with the external medium and only slowly with other root compartments such as the vacuoles, and it must release K^+ to the xylem directly. As the ER is a potential Na^+ pathway, the interconnected 'bulk cytoplasm' might be a possible route for symplastic K^+ movements. We suggest this cautiously, however. Simulation modeling (D Lazof, IM Cheeseman, unpublished results) indicates that this compartment cannot contain the amount of K^+ which the cytoplasm should and still have kinetics as rapid as those in Figure 3.

The general model for the acquisition and management of K^+ and Na^+ is, obviously, incomplete, and in the organismal context, the facts that it cannot explain are far more extensive than those it might. It does not, for example, suggest how the release of the ions from the symplastic compartments to the xylem occurs, or how it might be controlled. It says nothing of how the transport systems are integrated to produce the long-term similarities in net uptake rates and the apparent coregulation with growth that we have previously outlined (7).

Before committing the effort required to address such problems, however, we must recognize that the experimental system we have employed is an unusual one; we must question whether *S. marina* is an appropriate or physiologically relevant model system for other plants, particularly mesophytic crop species, or whether the data we have presented are characteristic only of an obscure and insignificant halophyte. We will address that question and extend our consideration of Na^+ and K^+ transport systems in the following paper (15), applying the experimental and analytical techniques to the study of transport in lettuce.

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