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Control of Na^+ and K^+ transport in *Spergularia marina*. II. Effects of plant size, tissue ion contents and root-shoot ratio at moderate salinity

John M. Cheeseman and Linda K. Wickens

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In this paper we continue our analysis of Na^+ and K^+ uptake in vegetative *Spergularia marina* (L.) Griseb. plants growing on 0.2× sea water in solution culture. We consider the relationships between isotope uptake and plant size, root: shoot ratio (RSR) and total ion contents, both individually (with the linear effects of time removed) and in combinations through stepwise multiple linear regression. The results differ from those of other studies, representing in our case inherent variability in a homogeneous population under steady-state growth conditions. The results were broadly similar for $^{22}Na^+$ and $^{42}K^+$. Total uptake was significantly and negatively correlated with RSR and root weight (W_r), and positively with root K^+ content (K_r). These 3 variables were mutually correlated, however, and this was reflected in the multiple analyses as a reduction or loss of significance of one or more of the measures. Transport to the shoot was very highly correlated with total uptake ($r^2 > 0.99$ for both isotopes), resulting in nearly identical regression results. In multiple regression analyses of root data alone, accumulation was related only to root contents, but in a manner inconsistent with the allosteric regulation hypothesis, the most significant correlation being positive with K_r. The results were nearly identical for the two isotopes. The results were not consistent with a single factor regulatory system involving only initial root plasmalemma ion influx. The observed Na^+-K^+ and root-shoot balances seem to require at least involvement of symplast-to-medium and symplast-to-xylem transport steps. Though the biochemical and biophysical signalling and transduction steps are not known, a physiological working hypothesis is presented, in which the positive correlation of uptake with root contents is balanced by a negative feedback signal deriving from plant size and by the diluting effects of growth. Considered over the vegetative period, these would produce the observed stability of plant contents during growth. The negative interaction with RSR is postulated to manifest the integrating system required to deliver ions to the shoot at the required rates.

Additional key words – Halophyte, ion transport, salt tolerance, transport regulation.

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, USA.

Introduction

In the previous paper (Cheeseman and Wickens 1986a) we began our analysis of the control of Na^+ and K^+ uptake and transport in *Spergularia marina* (L.) Griseb., emphasizing vegetative plants growing on moderately saline medium (0.2× sea water). We considered the hypothesis that transpiration had a significant influence on total ion uptake and transport to the shoot, and we concluded that such an effect was unlikely, both in short-term studies using isotope techniques to measure ion movements, and in longer-term studies using growth analysis.

A consequence of that study, at least for this experi-

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mental system, was that transpiration need not be considered in analyses of other plant factors affecting uptake and transport of these ions. Some factors which have been considered as single factors in other systems, are root age or size (Wiebe and Kramer 1954, Russell and Sanderson 1967, Rovira and Bowen 1970, Eshel and Waisel 1972, Harrison-Murray and Clarkson 1973), internal ion concentration (for a recent review see Glass 1983), and relative root and shoot size (e.g. Jeschke 1982). In the present paper we will consider the possible influence of those factors, alone and in combinations with other factors, on the uptake and internal partitioning of $^{22}Na^+$ and $^{42}K^+$ in mid-vegetative *S. marina* plants. All the plants were of the same age, with no differences in culture or experimental manipulation. Thus, our consideration will also differ markedly from other studies in that we are reporting effects and analyses related to inherent variability within a fairly homogeneous population rather than effects resulting from, for example, short- or long-term starvation, growth in unbalanced medium or root excision.

In a following paper, this analysis will be extended to consider longer-term controls and effects related to growth.

Abbreviations – C. V., coefficient of variation; K_r, Na_r, K_l, Na_l, root and shoot (leaf) Na^+ and K^+ contents expressed per gram fresh weight; RGR, relative growth rate; RSR, root: shoot ratio; W_r, W_l, W_t, root, shoot (leaf) and total plant weight; b, $\hat{b}$, regression coefficients (slopes) in simple and multiple linear regressions; ϱ, $\hat{\varrho}$, total and partial residuals; r, r', simple and partial correlation coefficients.

Materials and methods

Vegetative *Spergularia marina* (L.) Griseb. plants were used ca 17 days after transfer to solution culture and 7 days after salinization to 0.2× sea water. Details of culture techniques and growth conditions were outlined in the previous paper (Cheeseman and Wickens 1986a). Isotope procedures and tissue Na^+ and K^+ analysis methods were as described by Cheeseman et al. (1985a, 1985b). Plants were selected for uniformity of size at the time of transfer to solution culture. Therefore, variations between plants exploited in this study were those arising naturally during the subsequent growth period.

To some extent, the results which follow will depend upon the units chosen. Uptake of labeled ions will be expressed here in μmol (g fresh weight root)$^{-1}$. This is the commonly used basis in transport studies, and as it relates ion uptake to a physiologically meaningful and easily measured parameter, it is arguably the most satisfactory basis as well. Our results may be directly converted to uptake per unit root length or surface area using the conversion factors reported in Cheeseman et al. (1985a).

For the purposes of this analysis we will use the results of a single detailed time-course experiment performed in October, 1984. The uptake solution was double labeled but was otherwise identical to the growth solution. Harvests were spaced at 20 min intervals, with 3 or 4 samples per harvest. At harvest, plants were separated into roots, root/shoot interfaces and shoots for analysis. Interfaces represented less than 5% of the total plant and were not included in the analyses which follow. At the developmental stage of these plants, prior to elongation of branches, "shoot" and "leaves" were equivalent (Cheeseman et al. 1985a). All of the single parameter relationships which will be presented were found consistently in other experiments; this study was performed with more extensive data collection in order that all statistical comparisons could be made with a single data set.

Statistical analyses were performed using the BMDP statistical package (Dixon 1981). Linearity checks of the dependence of uptake on time were performed using polynomial regression. Selection of the appropriate degree was based on the significance of the F-statistic as defined in the Goodness-to-Fit test in that program (Dixon 1981, Program 5R).

Figure 3 is a plot of partial residuals, ϱ_j, vs values of the independent variable, x_j. The partial residuals are defined according to the equation

$$\hat{\varrho}_j = \varrho + \hat{b}_j \cdot x_j \qquad (1)$$

where ϱ is the total residual, $\hat{b}_j$ is the regression coefficient for variable j, and x_j is the value of variable j. This technique, discussed in detail by Larsen and McCleary (1972), provides information similar to that contained in residual plots, i.e. it allows detection of outliers and assessment of heterogeneity of variance and of the need for further transformation of a variable. Partial residual plots also allow visual assessment of the importance of a potential independent variable, i.e. its predicting power for the dependent variable in the presence of all other variables. Furthermore, non-linearity which would influence the value of the regression can be visually assessed as well (Larsen and McCleary 1972). Characteristic of these plots is that the correlation between $\hat{\varrho}_j$ and x_j is the partial correlation, r', for x_j in the complete regression, and the slope of the plot is the regression coefficient, $\hat{b}_j$. The intercepts are zero in all cases.

Multiple linear regressions involving more than two (i.e. time-plus-one) independent variables were performed using stepwise regression (Dixon 1981, Program 2R). Variables were entered (or removed) from the regression in a sequence of steps dependent upon the significance of their additive contribution to the multiple correlation coefficient. As a result, variables whose coefficients would not be statistically different from zero were not included in the final analyses. Loss or gain of significance during the progress of an analysis resulted from the complexities of the correlations of potential independent variables. Stepwise regression also allowed

independent subjective evaluation of the point to which the addition of variables was physiologically meaningful (see $^{42}K^+$ analysis, Tab. 3).

Results

Figure 1 shows the time course of total $^{22}Na^+$ and $^{42}K^+$ uptake by vegetative *S. marina* plants 17 days after transfer to solution culture, uptake being expressed per gram root. Curves were fit by polynomial regression, the appropriate degree being selected as described above. Linear regressions were sufficient for $^{22}Na^+$. $^{42}K^+$ uptake proceeded with a pronounced lag as previously described (Cheeseman et al. 1985b) and is shown as a quadratic regression. When data were restricted to times of 120 min or more, the slope of $^{22}Na^+$ uptake was unchanged and a linear fit was sufficient for $^{42}K^+$. Such linearity with time was important for the subsequent use of multiple linear regression analysis. That this restriction was reasonable was also suggested by the fact that the ratio of the resulting slopes (1.54) was very close to the ratios of whole plant Na^+ and K^+ contents (Cheeseman et al. 1985a).

The time-restricted data set was complete for 61 individual samples. Further analyses were based on the independent variables shown in Tab. 1 which summarizes the means, coefficients of variation and correlations between the variables. Despite the relatively low C. V. of RSR and all measures of total tissue ion concentrations, the ratio of the largest to smallest values for each of the variables was at least 1.6 (see Fig. 2), which proved sufficient to allow meaningful correlation analyses.

Significant correlations between the parameters in Tab. 1 will have, potentially, important consequences for multiple regression analysis. To be noted particularly are the high correlations between the the various size measures and between W_r, RSR and K_r. These relationships are plotted in Fig. 2, which also establishes that the values for each variable were well distributed about their respective means. Distribution analyses were performed for each of the variables in Tab. 1 to assure that distributions about the means were normal and that significant correlations were not due to outliers.

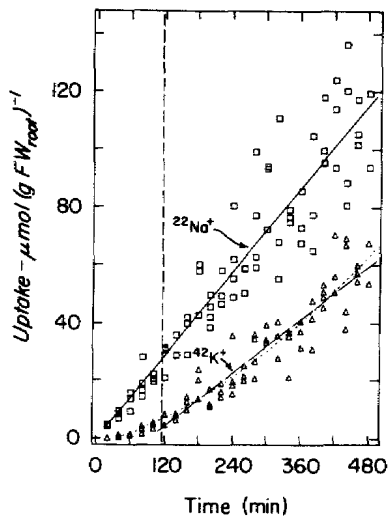
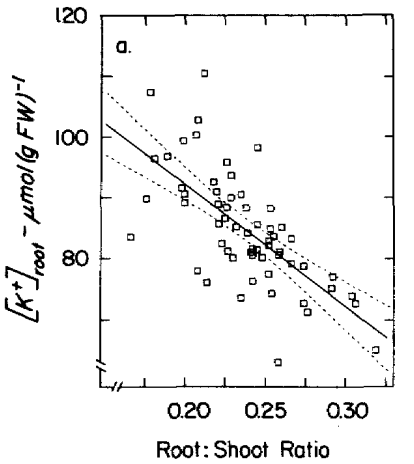


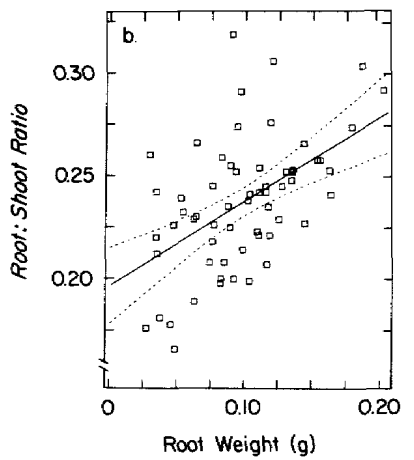
Fig. 1. The time course of $^{22}Na^+$ and $^{42}K^+$ uptake by mid-vegetative *S. marina* plants growing on 0.2× sea water, 17 days after transfer to solution culture. Solid line for $^{22}Na^+$ – least squares linear regression of uptake vs time. The intercept is zero, $r^2 = 0.783$, $b = 0.236 \pm 0.016$ [14.2 μmol $(g\ FW_{root})^{-1}\ h^{-1}$]. Dotted line for $^{42}K^+$ – quadratic regression for the full time course. The intrecept is again zero. Solid line for $^{42}K^+$ – linear regression for uptake vs time with data restricted to uptake times of 120 min (vertical bar) or longer; $r^2 = 0.854$, $b = 0.153 \pm 0.008$ [9.2 μmol $(g\ FW_{root})^{-1}\ h^{-1}$].

Table 2 shows the partial correlations (r') between $^{22}Na^+$ and $^{42}K^+$ uptake and the independent variables in Tab. 1 with the linear effects of time removed. Neither of the r' values with shoot Na^+ or K^+ content were significant, nor did they figure significantly in more complex regressions.

Tab. 1. General description of *S. marina* plants 17 days after transfer to solution culture. For each measure, the mean, coefficient of variation (C.V.) and correlation (r) to all other measures is given. The data set contained 61 observations. Critical r values for 0.05, 0.01 and 0.001 significance levels are 0.250, 0.325 and 0.408, respectively. W_r, W_l and W_t are in g FW. Contents are in μmol $(g\ FW)^{-1}$.

Parameter	Mean	C.V. (%)	Correlations							
			W_r	W_l	W_t	RSR	Na_r	K_r	Na_l	K_l
W_r	0.098	41	1							
W_l	0.382	37	0.957	1						
W_t	0.507	37	0.972	0.998	1					
RSR	0.237	13	0.526	0.282	0.331	1				
Na_r	61.6	12	–0.609	–0.524	–0.548	–0.519	1			
K_r	84.6	11	–0.518	–0.342	–0.386	–0.754	0.664	1		
Na_l	130.8	13	–0.546	–0.583	–0.580	–0.108	0.414	0.037	1	
K_l	122.4	12	–0.017	–0.091	–0.077	0.203	0.063	–0.140	0.143	1





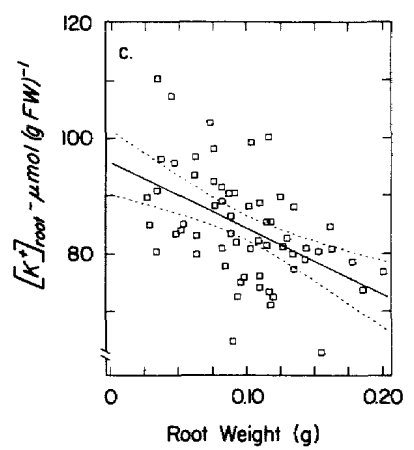


Fig. 2. The relationship between the independent variables root weight (W_r), root: shoot ratio (RSR), and root K^+ concentration (K_r), in mid-vegetative *S. marina* plants growing on 0.2× sea water. Linear regressions (solid lines) and 95% conables. Correlation coefficients are given in Tab. 1. a, ables. Correlation coefficients are given in Tab. 1. a, K_r vs W_r; b, RSR vs W_r; c, K_r vs RSR.

Tab. 2. Partial correlations (r′, with the linear effects of time removed) between (a) total $^{42}K^+$ and $^{22}Na^+$ uptake shown in Fig. 1 and (b) root retention of labels, with descriptive measures of vegetative *S. marina* plants from Tab. 1. Critical r′ values for 0.05, 0.01 and 0.001 significance levels were 0.250, 0.325 and 0.408 respectively. Uptake units were µmol (g $FW_{root})^{-1}$. Uptake times were restricted to 120 min or longer.

Parameter	Partial correlations (r′)			
	Total uptake		Root accumulation	
	$^{42}K^+$	$^{22}Na^+$	$^{42}K^+$	$^{22}Na^+$
W_r	–0.415	–0.570	–0.247	–0.355
W_l	–0.272	–0.449	–0.100	–0.223
W_t	–0.300	–0.471	–0.132	–0.254
RSR	–0.697	–0.742	–0.587	–0.559
Na_r	0.240	0.319	0.213	0.506
K_r	0.682	0.589	0.699	0.653
Na_l	–0.129	0.181	–0.180	0.144
K_l	–0.166	–0.083	–0.170	–0.121

Potassium

As controlling factors for K^+ uptake have been the subject of discussion for many years, we were particularly concerned with the relationship between that rate and W_r, RSR and K_r. Those relationships were analyzed individually in combination with time. Table 3 summarizes the regression parameters for the separate analyses. The coefficient for time was not altered significantly from that shown in Fig. 1. Figure 3 shows the partial residual plot for each regression, indicating that $^{42}K^+$ uptake was linearly related to all 3 variables, and that the results did not depend on unusual distributions or outliers. The correlations were negative for W_r and RSR, and positive for K_r.

The high mutual correlations between the variables in Tab. 1 raised the question of the degree of importance each factor had independent of the others. Therefore, we proceeded with a stepwise multiple regression of $^{42}K^+$ as a function, potentially, of all the variables in Tab. 1. Progress of this analysis may be conveniently divided into two stages. In the first, after inclusion of time, the more significant variables in Tab. 2 were considered (RSR, K_r and W_r). After inclusion of RSR, r′ for K_r decreased substantially, and the partial correlation with W_r was no longer significant (r′ = −0.080). No new variable of significance appeared. Inclusion of K_r resulted in a decrease in the level of significance for

Tab. 3. Regression parameters for time-plus-one variable multiple linear regression analyses of $^{42}K^+$ and $^{22}Na^+$ uptake in the experiment shown in Fig. 1. Uptake times were restricted to 120 min or longer. Regression coefficients ($\hat{b}$), SE of the coefficients, and multiple r^2 values are given for each "plus-one" variable. r^2 for regression using time as the only independent variable was 0.854 for $^{42}K^+$ and 0.783 for $^{22}Na^+$.

Parameter	Regression results					
	$^{42}K^+$			$^{22}Na^+$		
	$\hat{b}$	SE	mult. r^2	$\hat{b}$	SE	mult. r^2
W_r	−71.3	20.5	0.879	−193	36	0.853
RSR	−155	21	0.925	−325	39	0.902
K_r	0.513	0.072	0.922	0.870	0.157	0.858
Na_r	–	–	–	0.611	0.236	0.804

Tab. 4. Results of multiple linear regression analyses of total $^{42}K^+$ and $^{22}Na^+$ uptake in the experiment shown in Fig. 1, with uptake times limited to 120 min or longer. All measures in Tabs 1 and 2 were available to the stepwise analysis. Regression coefficients ($\hat{b}$), SE of the coefficients, and partial correlation coefficients in the final regression are given for each significant variable.

Parameter	Regression results					
	$^{42}K^+$			$^{22}Na^+$		
	$\hat{b}$	SE	r′	$\hat{b}$	SE	r′
Time	0.151	0.007	0.950	0.211	0.009	0.949
W_r	–	–	–	731	204	0.434
W_l	–	–	–	−73.1	17.2	−0.496
RSR	−94.2	30.4	−0.380	−605	82	−0.707
K_r	0.273	0.103	0.333	–	–	–
Na_r	–	–	–	−0.520	0.178	−0.366
Intercept		−14.3			197.1	
Multiple r^2		0.933			0.940	

RSR. Both this and the loss of W_r above reflect the correlations between the 3 parameters (Fig. 2). At this point, which may be considered the end of the first stage, $r^2 = 0.933$.

Inclusion of K_r resulted in an increase in the significance of Na_r ($r' = -0.436$). Note that the sign of r′ was reversed from that in Tab. 2. In subsequent steps W_l and W_r were added, their relative significance and the sign of the coefficient for W_r being reversed (W_r: $r' = 0.295$, $\hat{b} = 254$; W_l: $r' = -0.333$, $\hat{b} = -24.6$). The final multiple r^2 increased to 0.954 in the second stage of the analysis. We consider that these stage 2 inclusions and changes, and particularly the off-setting effects of W_r and W_l, represent statistical "fine-tuning" of the regression, with no clear physiological meaning. Therefore, we terminated the analysis with inclusion of K_r (stage 1) and the results are summarized in Tab. 4.

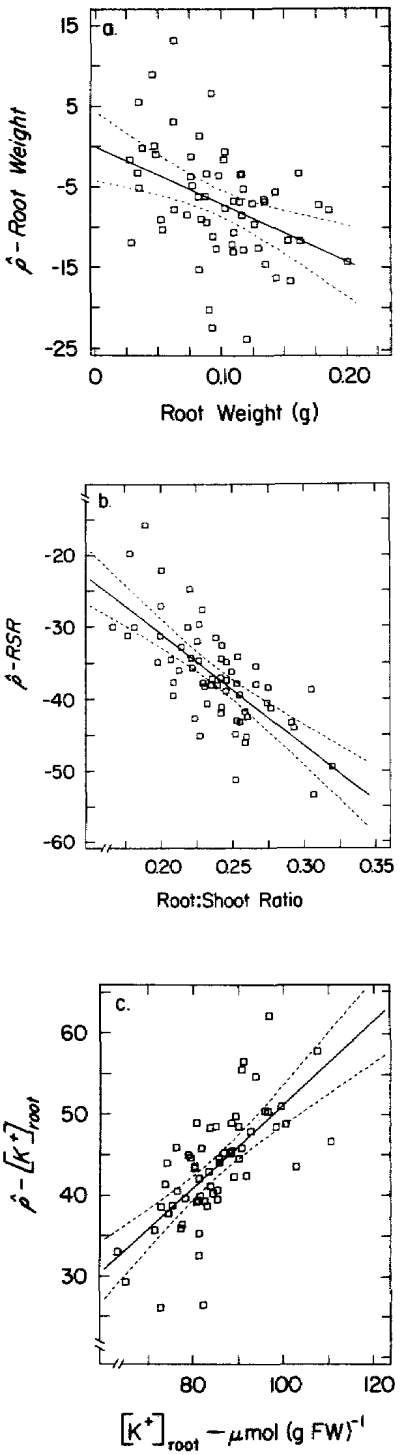
Sodium

$^{22}Na^+$ uptake data were analyzed in a similar manner. Values of r′ were significant for W_r, W_l, W_t, RSR, K_r and, marginally, for Na_r (Tab. 2). The highest significance corresponded to the same variables discussed for $^{42}K^+$ above. Regression parameters corresponding to those time-plus-one regressions in Fig. 3 are shown for $^{22}Na^+$ in Tab. 3; all relationships were linear. Also shown are the values for the regression including time-plus-Na_r (also linear). The regression coefficients were substantially greater in the $^{22}Na^+$ than in the $^{42}K^+$ analysis.

Stepwise analysis proceeded without the two clearly distinct phases discussed above (Tab. 4). Inclusion of both W_r and W_l was considered to signify only dependence on plant size; prior to inclusion of either, the r′ values were very similar and negative. Inclusion of Na_r is more intuitively reasonable here than it was for $^{42}K^+$, though there was again an unexplained sign reversal. Exclusion of Na_r resulted in only minor changes in the coefficients and partial correlation coefficients for the other parameters.

Internal distributions

Accumulation of $^{22}Na^+$ and $^{42}K^+$ by roots and transport of the labeled ions to the shoots were considered separately by repeating the above analyses for label in the shoots and roots at each harvest. The correlations be-



tween shoot and total contents for $^{22}Na^+$ and $^{42}K^+$ respectively were 0.993 and 0.998 and there were, therefore, only minor differences from the results already presented. Internal partitioning was also considered based on the percentage of the total label in the shoot at harvest. In both cases, partitioning reached a steady level at a rate which was well described by a cubic polynomial function of time (r^2 = 0.93 in both cases; see Cheeseman and Wickens 1986a; Fig. 5). With the time effects removed, no significant improvement in r^2 resulted from inclusion of other independent variables.

Results for root accumulation were substantially different. Table 2 shows the partial correlations between root accumulation rates and the descriptive measures as were discussed above for total uptake. Again, the variables most significantly correlated to accumulation were RSR, K_r (and Na_r) and W_r, though the significance of W_r was marginal and the relative significance levels of RSR and K_r were reversed. In multiple regression analyses, these differences, in combination with the mutual correlations of the independent variables, were sufficient to prevent addition of RSR or size measures after inclusion of K_r. The final results, strikingly similar for the two ions, are summarized in Tab. 5. The negative coefficient for Na_r again represented a sign reversal.

Discussion

In this study, we have considered the control of Na^+ and K^+ transport in *Spergularia marina* at the whole plant level under steady-state conditions. Rather than generating variability by altering the nutrient balance of the growth medium in a pretreatment period, we have started with uniform seedlings and exploited the variability which occurred naturally thereafter.

For both ions, total uptake was highly correlated to plant size, to RSR and to root ion contents, especially K^+ (Tab. 2). The negative correlation of the uptakes with root weight reflects a quadratic dependence of total uptake (per plant basis) on root weight (data not shown). Some dependence of uptake per unit root on root system size has also been indicated by numerous studies of isolated root lengths (see Introduction) and, more recently, by the preliminary report of Kochian and Lucas (1985) of standing diffusion gradients along corn roots in "convection damped" solutions. The quantitative importance of such studies to whole system uptake rates has, however, not been well defined.

Fig. 3. Partial residual plots indicating the effect on $^{42}K^+$ uptake of (a) W_r, (b) RSR, and (c) K_r in vegetative *S. marina* plants on 0.2× sea water. Each of the plots indicates the predicting power of the independent variable (with 95% confidence interval indicated by dashed lines) in two variable (time-plus-one) multiple linear regression analyses with the effects of time removed. Data were restricted to times of 120 min or longer. Parameters for time-alone regressions are given in Fig. 1. Partial correlations (r') are given in Tab. 2. Coefficients and multiple r^2 values are given in Tab. 3.

Tab. 5. Results of multiple linear regression analysis of root accumulation of $^{42}K^+$ and $^{22}Na^+$. Uptake times were restricted to 120 min or longer. Regression procedures were identical to these in Tab. 4.

Parameter	Regression results					
	$^{42}K^+$			$^{22}Na^+$		
	b	SE	r'	b	SE	r'
Time	0.0472	0.0015	0.972	0.0457	0.0027	0.907
K_r	0.209	0.023	0.763	0.210	0.032	0.653
Na_r	–0.121	0.030	–0.469	–	–	–
Intercept		–13.8			–14.6	
Multiple r^2		0.947			0.833	

For $^{42}K^+$ the non-linearity was not enough to affect the multiple regression dramatically, instead being more a question of marginally significant improvement in r^2. The negative effect of one measure was largely offset by the subsequent positive effect of the other. In the $^{22}Na^+$ analysis the partial correlations after removing only the linear effects of time (Tab. 2) were greater than for K^+, reflecting a somewhat greater dependence of Na^+ uptake on plant size. This size effect remained visible in the final regression, though with the same off-setting effect of including both W_r and W_l.

A high correlation between K_r and uptake of $^{42}K^+$ has in other studies (see Glass 1983) given rise to the hypothesis of allosteric regulation of uptake. Like the recent report of Drew and Saker (1984) for barley, our results suggest that there was no such regulation in this system; there was a positive rather than a negative correlation between $^{42}K^+$ uptake and K_r (Fig. 3c, Tab. 2). When root accumulation alone was considered (Tab. 5), the positive correlation with K_r was still more significant. The low C.V. associated with K_r should, however, be acknowledged (Tab. 1). A positive uptake vs K_r dependence was also shown for several species by Jensén and Pettersson (1978) and Pettersson and Jensén (1978) for K^+, but only in severely depleted seedlings.

On the other hand, a negative feedback effect of Na_r on $^{22}Na^+$ uptake appeared in the final regressions, both for whole plant uptake and for root accumulation. This relationship was only found after removing the linear effects of the other variables. This suggests that in single factor analyses such as those used in most studies, allosteric regulation may, perhaps, be apparent only in very restricted conditions. Further attention to this hypothesis of transport regulation in fully autotrophic, balanced nutrient systems is clearly, required.

For both total $^{22}Na^+$ and total $^{42}K^+$ uptake, the most significant factor in simple or complex multiple regressions (other than time) was RSR. Jeschke (1982) considered the effect of surgically altered RSR in very young barley seedlings and found a similar negative correlation to uptake. There are, unfortunately, no other studies known to us which have considered the influence of that parameter. Here, the relatively small variability of RSR and the strong dependence of uptake on RSR support, in principle, the hypotheses of a functional equilibrium between root and shoot size as suggested by Brouwer (1983), and the involvement of RSR in response to nutrient stress as discussed by Chapin (1980).

Thus, the present results corroborate a number of other studies so long as single factor correlations are considered. Those factors had, however, high mutual correlations (Tab. 1) which have not previously been considered in any study. Analysis of uptake accounting for those correlations suggests how we might combine our results with several generally known but poorly understood characteristics of plant nutrition to develop a broad working hypothesis for future studies. In particular, any integrated ion transport model will have to recognize that the majority of a plant's nutrients are in the shoot. In general, this would probably include Na^+, despite notable exceptions in agronomically important species. In *S. marina*, more than 80% of the Na^+ and K^+ are in the shoot throughout the vegetative phase (Cheeseman and Wickens 1986a). Furthermore, nutrients are for the most part aquired and partitioned internally as needed for growth (Chapin 1980, Clarkson and Hanson 1980). In *S. marina*, Na^+ conforms to this role as well (Cheeseman and Wickens 1986b).

There are additional features which make the problem of Na^+ and K^+ regulation particularly interesting in this system. *S. marina* is a rapidly growing annual found naturally in a high resource, coastal salt marsh environment. Its K^+ acquisition and H^+ efflux patterns typify a ruderal strategy (Chapin 1980, Cheeseman and Enkoji 1984, Cheeseman et al. 1985b), apparently mediated by the same sort of K^+, H^+-ATPase as has been postulated for such plants. On the other hand, *S. marina* is highly salt tolerant, and even at full sea water salinity it is an effective Na^+ excluder (Cheeseman et al. 1985a).

The results of whole plant ion analyses (Cheeseman et al. 1985a), supported by the results of multiple regression analyses (Tabs 4 and 5), indicate that despite these basic differences, the systems operate with similar

controls. The net result is that even with a 45-fold excess of Na^+ over K^+ in the growth medium, the internal Na^+ and K^+ contents are similar, both in the roots and in the shoots (Tab. 1).

Thus, these results argue against the existence of a regulatory system simply involving the initial plasmalemma influx step. At the least, a suitable model to account for the Na^+-K^+ and root-shoot balances should probably involved efflux from the root symplasm to the medium and transport to the xylem. The combination of a positive dependence of uptake on contents and a low variability of both K_r and Na_r (Tab. 1) implies existence of a multi-component control system, since positive feedback alone would tend to accentuate differences and increase variability of contents between plants. The high, negative correlations between root contents and W_r (Fig. 2c, Tab. 1) suggests that the unbalancing effects of positive feedback may be opposed by a negative feedback signal deriving from size, and by the diluting effects of growth. Considered over a longer time period, these interactions could result in stabilization of contents during growth. Finally, a negative interaction involving RSR could manifest the integrating system required to deliver ions to the shoot at the required rates.

Clearly, this discussion provides no hint of the actual regulatory mechanisms or of the signals linking them to the significant regression parameters. We have also clearly not exhausted the list of possible correlates influencing the control systems, or of the nutrients which may be similarly controlled. Nevertheless, the factors which we have considered maintain their place as basic measures at least through the vegetative phase. We will consider their relationship to ion uptake and growth of *S. marina* in the following paper (Cheeseman and Wickens 1986b).

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