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Control of Na^+ and K^+ transport in *Spergularia marina*. III. Relationship between ion uptake and growth at moderate salinity

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In this paper, we continue our analysis of Na^+ and K^+ uptake by mid-vegetative *Spergularia marina* (L.) Griseb. plants growing on 0.2× sea water medium, with attention to the relationship of ion uptake and growth. In the first part of the paper, growth analysis techniques are used to compare relative growth rates (RGR) and relative accumulation rates (RAR) for Na^+ and K^+. Under constant growth conditions, a high correlation between RGR and RAR indicated that growth and accumulation of both ions were well balanced, resulting in Na^+ and K^+ concentrations within the plants which were stable after adjustement to the saline medium. The analysis confirmed the existence of a Na^+-related growth stimulation in *S. marina* and an associated increase in the efficiency of K^+ utilization for growth. When plants were subjected to more rapid salinization and step changes in the light intensity of the growth chamber, RGR and RAR were again similar, even through the discontinuities in growth conditions, suggesting that growth and ion accumulation were co-regulated rather than simply correlated.

The growth analysis data were then transformed to give net uptake rates for Na^+ and K^+ and the results were compared to those of isotope studies under similar growth conditions. In roots, the rates estimated by the two techniques differed substantially; net uptake rates reflected primarily growth, while isotope studies indicated a substantial ion exchange rate between mature cells and the growth medium. The rates of transport of either Na^+ or K^+ to the shoot were very similar using the two estimation techniques. As the rates measured with isotopes were taken from studies lasting at most a few hours, this suggested a very rapid turnover of the upwardly mobile Na^+ and K^+ pools in the roots.

Additional key words – Growth analysis, halophyte, ion transport, salt tolerance.

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Introduction

In our previous papers we have considered the control of Na^+ and K^+ transport in intact, vegetative *Spergularia marina* (L.) Griseb. plants growing under steady-state conditions in solution culture and at moderate salinity (Cheeseman and Wickens 1986a,b). We suggested, based upon the observed correlations between the uptake of $^{22}Na^+$ and $^{42}K^+$ and independent measures of plant size, tissue ion contents and root:shoot ratio (RSR), a working hypothesis by which the plants could maintain relatively constant internal conditions during growth, at least through the vegetative period. Control of Na^+ and K^+ uptake was hypothesized to involve negative feedback based upon plant size and RSR, and positive feedback involving root ion levels.

Those studies were, however, limited to consideration of plants at a single age, 17 days after transfer to solution culture and 7 days after salinization. To explore the hypothesis and to consider the physiological end result of the putative control network, the ionic relations of the plants must be understood in the context of

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growth. Ion accumulation must be analyzed in such a way that short-term isotope and longer-term net accumulation can be compared. Unfortunately, the majority of the studies which have considered ionic relations and growth have not been reported such that those comparisons are possible. However, as Nye and Tinker (1969) noted in their development of the concept of the root absorption coefficient, such data must exist; ion contents and plant weights are routine components of a variety of agricultural and ecological analyses. It was, presumably, due to this lack of data transformed as required, that the recent review of transport regulation by Glass (1983) did not consider growth, and that Moorby and Besford (1983) cited, in this regard, only the study of Pitman (1972).

In the present paper we will analyze the accumulation of Na^+ and K^+, and the growth of *S. marina* plants at moderate salinity during the mid-vegetative period, i.e. from the time of salinization to the onset of branch elongation. Using growth analysis techniques, the correlation between ion accumulation and growth will be analyzed first. Second, the accumulation of Na^+ and K^+ will be expressed in the units common to ion transport studies and uptake estimates using isotope and growth analysis methods will be compared.

Abbreviations – CV, coefficient of variation; NUR, net uptake rate; RAR_j, relative accumulation rate for ion j; RGR, relative growth rate; RSR, root:shoot ratio; SUR, specific utilization rate.

Materials and methods

Spergularia marina seeds were collected from plants growing in our growth chambers and were germinated, transferred to solution culture, and grown as described in detail in part I of this series (Cheeseman and Wickens 1986a). The experimental methods and analytical techniques used for $^{42}K^+$ and $^{22}Na^+$ studies were as described by Cheeseman et al. (1985b). Plants used in growth study and isotope experiments were treated identically with the exception that humidity, which could not be controlled, was somewhat higher in the growth studies (performed in the summer) than in the isotope studies (performed in the autumn and winter).

Analyses of plant growth and net ion accumulation rates were based on data from frequent small harvests (Hunt 1982). The present paper will use two such studies extensively. The first study was performed in May and June 1984. Seedlings were carefully selected for uniformity and transferred to solution culture ca 2 weeks after germination. Salinization to 0.2× sea water followed the schedule presented previously (Cheeseman and Wickens 1986a). The plants were grown under uniform environmental conditions thereafter; ages refer to days after transplanting. Harvests began on day 11. Five plants were harvested daily until day 20, then on days 22, 25 (beginning of branch elongation) and 35 (first flowering). Plants to be harvested were randomly selected from the remaining population, and all plants were eventually harvested.

At harvesting, roots were rinsed in ice-cold $CaCl_2$ (20 mol m^{-3}) for 10 to 15 min. Aerial parts were rinsed briefly in the same solution. Plants were divided into roots, shoots and root/shoot interfaces for analysis. Parts were weighed, dried, re-weighed and ashed at 500 to 525°C for 3 h. Ashed samples were re-suspended in 1000 mol Mg-acetate m^{-3} at a dilution ratio of ca 0.1 g dry weight ml^{-1}. Samples were vortexed briefly 15 min prior to analysis and allowed to settle. Na^+ and K^+ content were determined by flame emission spectroscopy.

Growth was described using the computer programs of Hunt and Parsons (1981). The age dependence of plant size was fitted to an equation of the form:

$$\ln(W_d) = a + b_1 \cdot t + \ldots + b_n \cdot t^n, \qquad n \leqq 3 \qquad (1)$$

where W_d is the dry weight of the plant or plant part and t is age.

The accumulation rates of Na^+ and K^+ were described similarly by substituting M_{Na} or M_K (mol of Na^+ or K^+) for W_d in eq. (1).

The first derivative of eq. (1) is the relative growth rate (RGR) or, for Na^+ or K^+, the relative accumulation rate (RAR_{Na}, RAR_K) and is defined by the equation:

$$RGR = \frac{1}{W_d} \cdot \frac{dW_d}{dt} = b_1 + 2 \cdot b_2 t + 3 \cdot b_3 \cdot t^2 \qquad (2)$$

Clearly, if $n < 3$ in eq. (1), eq. (2) will be simplified accordingly, and if growth is strictly exponential, $RGR = b_1$. Substitution of M_j for W_d in eq. (2) defines RAR_j.

Analyses of RGR based on fresh weight gave similar results, as the moisture content of the plants was 91.3±0.06% regardless of plant age and with no significant differences between plant parts.

From fitted regressions of the form in eq. (1) the specific utilization rates (SUR) and the net uptake rates (NUR) can also be calculated (Hunt 1982). The general form of the functions is similar.

$$SUR = \frac{1}{M_j} \cdot \frac{dW_d}{dt} \qquad (3)$$

and

$$NUR = \frac{1}{W_r} \cdot \frac{dW_j}{dt} \qquad (4)$$

SUR indicates the efficiency of nutrient use in total dry matter production. In the present paper, we are concerned with a K^+-sparing effect of Na^+ and, thus, will limit our analysis of this function to K^+. Equation (4) is used in the comparison of net ion accumulation and iso-

tope uptake rates. For this reason, NUR analyses will be based on root fresh weight, W_r. With the constant external concentrations used in these studies, NUR was directly proportional to the root absorption coefficient, α, as defined by Nye and Tinker [1969, eq. (4)]. This reflects our observations that (a) the mean root radius was constant with root system size, and (b) root length was directly proportional to weight (Cheeseman et al. 1985a).

The second growth study, used for Fig. 5, was performed in July and August 1984. For this study, plants were salinized on day 13 to 0.1x sea water at 11 00 h after the harvest for the day, and to 0.2× sea water at 17 00 h. At day 16, the growth chamber light intensity was decreased from 500 to 90 µmol m^{-2} s^{-1} by turning off 27 of 32 fluorescent tubes. Intensity remained at the lower level with the same 14 h photoperiod until day 32 when it was restored to the initial level. The change in light intensity was accompanied by other, uncontrollable changes in the growth chamber environment, including a change in the heat load of the chamber and therefore of the growth medium temperature. Consideration of the effects of the altered conditions will, therefore, be limited to areas in which the complexities are unimportant.

Because of the discontinuities in the growth conditions, the continuous equation analysis used for the first study was not acceptable. RGR and RAR were calculated, instead, using discrete overlapping estimations. For each time period, RGR was defined as:

$$RGR = \frac{\ln (W_d)_{n+2} - \ln (W_d)_n}{t_{n+2} - t_n} \quad (5)$$

W_d is the mean dry weight of the 5 samples at each harvest. For RAR_j, M_j was substituted for W_d. The procedure of skipping harvests (i.e. of using harvests n and n+2 instead of n and n+1) and overlapping estimation periods was adopted in order to smooth the curve somewhat, eliminating variation associated with the sampling alone, and at the same time preserving the major variations which were associated with salinization and light intensity changes. This technique is similar in concept to, but simpler in practice than, the "running re-fit" method discussed by Hunt (1982).

Results

Ion accumulation and growth

The growth of *Spergularia marina* following salinization during the early vegetative period to 0.2× sea water was not strictly exponential, but decreased with age to the beginning of branch elongation. In the formalism of growth analysis [eq. (1)], the regression coefficients b_2 and b_3 were non-zero. Consequently, RGR [eq. (2)] was not constant, but decreased with age as well. Similar results were obtained for the net accumulation of Na^+ and

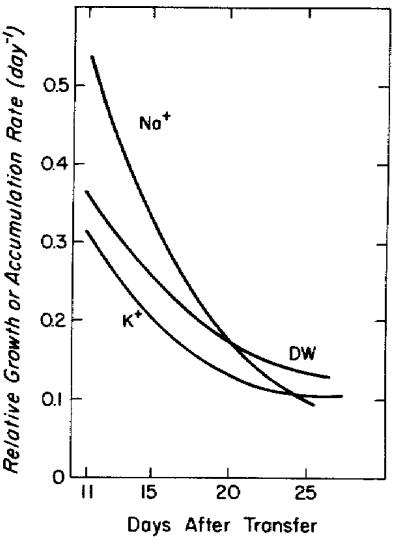

Fig. 1. Age dependence of relative growth rate (RGR) on a dry weight basis, and relative accumulation rates (RAR) for Na^+ and K^+ in *Spergularia marina* plants following transfer to solution culture and salinization to 0.2× sea water. Salinization was complete at 10 days after transfer. Curves are fitted results of growth analysis using the stepwise program of Hunt and Parsons (1981).

K^+. Figure 1 compares RGR, RAR_{Na} and RAR_K from vegetative *S. marina* over this period. The first harvest, at day 11, was made 45 h after the beginning of salinization and 19 h after the increase to 0.2× sea water; the high initial RAR_{Na} reflects the initial acquisition of Na^+. Following day 18, RAR_{Na} and RGR were not significantly different. RAR_K was slightly lower than RGR throughout the period although the difference was statistically significant only between days 14 and 20.

These differences were reflected in changes in concentrations of Na^+ (increasing) and K^+ (decreasing) in the plants. In the leaves, however, the total monovalent cation concentration remained constant throughout the period (Fig. 2). Because more than 80% of the total Na^+ and K^+ were in the leaves, the leaf and whole plant patterns were similar. These changes indicated a Na^+-for-K^+ replacement, but also reflected a dilution of K^+ during growth that occurred even in the absence of Na^+. Table 1 compares the K^+ levels at days 11 and 17 after transfer to solution culture for plants grown on Na-0 and 0.2× sea water media. The average, whole plant K^+ concentration decreased by 32% in the salinized plants, but also decreased by 15% in the absence of Na^+ (the Na-0 data are based on a similar growth analysis). The relative growth rates are compared in the center columns of Tab. 1. RGR was lower at both ages decreased proportionately more with age under Na-0 conditions. This verified our earlier report of Na^+-stimulated

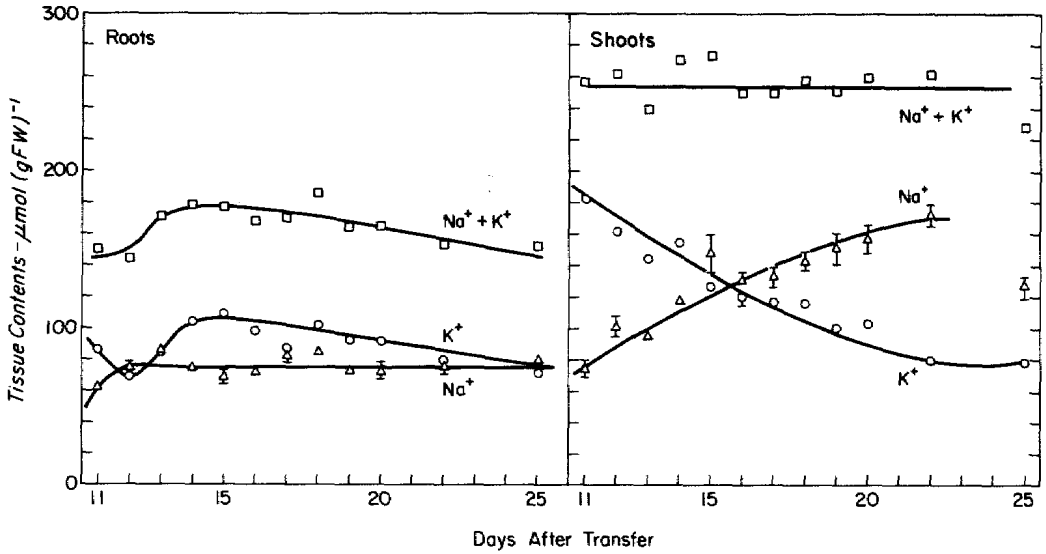

Fig. 2. Na^+ (Δ), K^+ (○) and Na^+ *plus* K^+ content (□) of roots and shoots of mid-vegetative *S. marina* plants. Results are expressed as µmol (g FW)$^{-1}$. Each point is the mean ± SE of 5 samples. Error limits not shown were smaller than the symbols. Lines were placed without regression, to serve as visual guides only.

growth in *S. marina* (Cheeseman et al. 1985a), and indicated that the decrease in RGR with age in Fig. 1 did not represent a growth-inhibiting effect of salinity.

The Na^+-related dilution of leaf K^+ with growth (Fig. 2) also represented an increase in the specific utilization rate (SUR) for K^+ [eq. (3)], or a K^+ sparing effect of Na^+. As shown in the final columns of Tab. 1, the SUR was higher at both ages and decreased less with age in the salinized plants.

A different pattern of Na^+ and K^+ tissue concentrations was found for roots. The Na^+ content reached a steady level by day 12, within 72 h of the beginning of salinization. K^+ content declined transiently, then more gradually to the onset of branch elongation. Total monovalent cation content of roots, therefore, mirrored the changes in K^+ (Fig. 2).

The percentage of the total K^+ which was in the shoots decreased with age, from 86% at day 11 to 72% at day 25. The percentage of the total Na^+ in the leaves increased slightly from 79% at day 11 to 89% at day 15, then decreased despite stabilization of both root and shoot concentrations (Cheeseman and Wickens 1986a). This decrease largely reflected an increase with age of the root:shoot ratio after day 15 (Fig. 3).

Recirculation of Na^+ from the shoots to the roots for subsequent active excretion could also contribute significantly to these observations and could have a significant effect on interpretation of isotope results. Two different types of experiments, however, indicated that such recirculation does not occur in this system. First, plants labeled for the first 7 days of salinization with $^{22}Na^+$ in the growth medium (0.2× sea water) showed no loss of label and less than 5% redistribution to new shoot tissue in a following 14-day period without label (data not shown). Second, plants grown for 14 days on 0.4× sea water showed no loss of Na^+ from either roots

Tab. 1. Comparison of total plant K^+ content, relative growth rate and K^+ specific utilization rate in mid-vegetative *S. marina* plants growing on Na-0 or 0.2× sea water medium. Values are compared at 11 and 17 days after transfer to solution culture. Contents are means ± SE; n = 5. RGR and SUR are fitted estimates ± SE.

Age days	Contents, µmol K^+(g FW)$^{-1}$		RGR, day^{-1}		SUR, g DW (mol K^+)$^{-1}$ day^{-1}	
	Na-0	0.2×	Na-0	0.2×	Na-0	0.2×
11	183±1	164±4	0.22±0.01	0.36±0.03	124± 9	201±15
17	156±3	111±2	0.11±0.01	0.22±0.01	59±10	169± 5

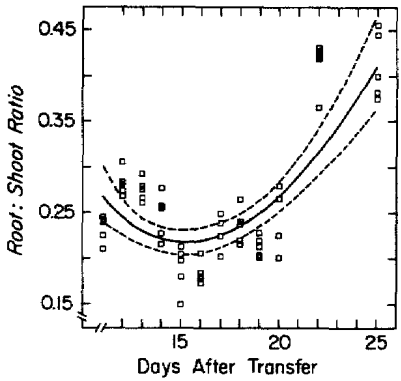

Fig. 3. Age dependence of root:shoot ratio (RSR) of mid-vegetative *S. marina* plants from completion of salinization to 0.2× sea water to the beginning of branch elongation. Symbols represent individual samples. Solid line was fit by polynomial regression (cubic) to the individual sample values. Dotted lines – 95% confidence interval for the regression line.

or shoots following an additional 13 days growth on Na-0 medium (Tab. 2). Table 2 also implies that Na^+ cannot be exchanged for K^+ or other cations.

For both ions, these results could simply indicate a correlation between growth and ion uptake, or they might indicate that the processes were well-integrated and similarly regulated. Figure 4 illustrates the results of an experiment challenging and supporting this latter possibility.

Growth and net ion accumulation were measured through 3 treatment discontinuities, i.e. salinization and 2 illumination changes, using the discrete overlapping estimate technique (see Materials and methods). Though RAR_{Na} was very high upon initial exposure to NaCl, the rapid salinization in this experiment resulted in a transient reduction of growth and of accumulation rates for both ions. Transient reductions also accompanied the changes in light intensity. Recovery of the whole plant balanced growth was complete at low light, and following day 22, RGR, RAR_{Na} and RAR_K were similar and relatively constant. Recovery was more rapid following the return to high light and the rates rose to a level similar to those in control plants at the same developmental stage (data not shown). The final divergence of growth and accumulation rates after day 37 is unexplained but may have been associated with the approach to flowering which, under these conditions, began at day 42.

Tab. 2. Na^+ content of *S. marina* plants following 14 days growth on 0.2× sea water and a subsequent 13 days growth on Na-0 medium. Plants were transferred to 0.4× from 0.2× sea water on day 11, and were returned to Na-0 medium in a single step on day 25. Na-0 medium was carefully monitored and changed frequently to avoid continued Na^+ uptake. Data are means ± SE. Root/shoot interfaces were included in the total content analyses.

Age days	Na^+ content μmol (plant)$^{-1}$		
	Roots	Shoots	Total
25	12±1 (10)	221±14 (10)	237±15 (10)
38	25±4 (8)	210±29 (8)	247±33 (8)

Comparison of net accumulation and isotope uptake

To understand the growth study results in the termi-

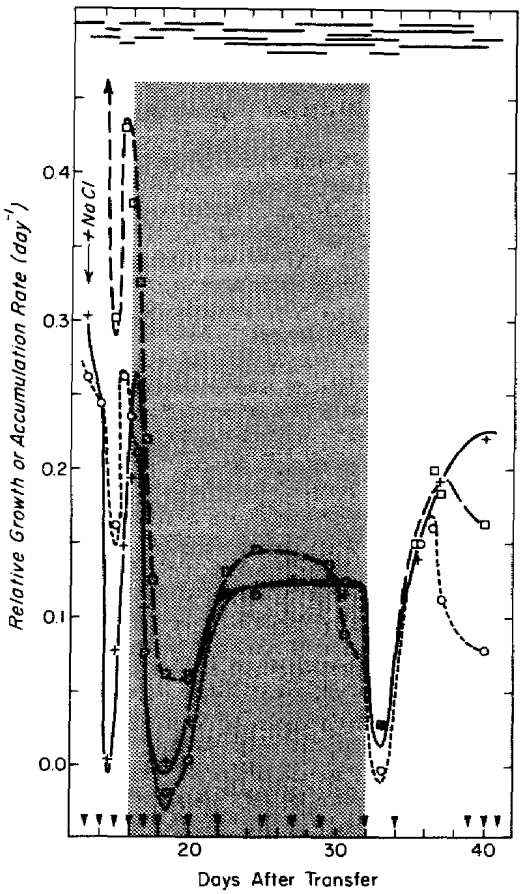

Fig. 4. Relative growth rates (+) and relative accumulation rates for Na^+ (□) and K^+ (○) in the second growth study. The medium was salinized to 0.2× sea water on day 13 (arrow, +NaCl). Growth chamber light intensity was reduced from 500 to 90 μmol m^{-2} s^{-1} for the period designated by shading. Harvest days are indicated with arrowheads on the x-axis. Points were determined using the discrete overlapping estimate technique (see Materials and methods). Intervals covered by the points are shown as horizontal bars at the top of the graph. Lines were smoothed to the points to serve as guides. The very high initial value of RAR_{Na} reflects initial accumulation of Na^+ by previously Na^+-free plants.

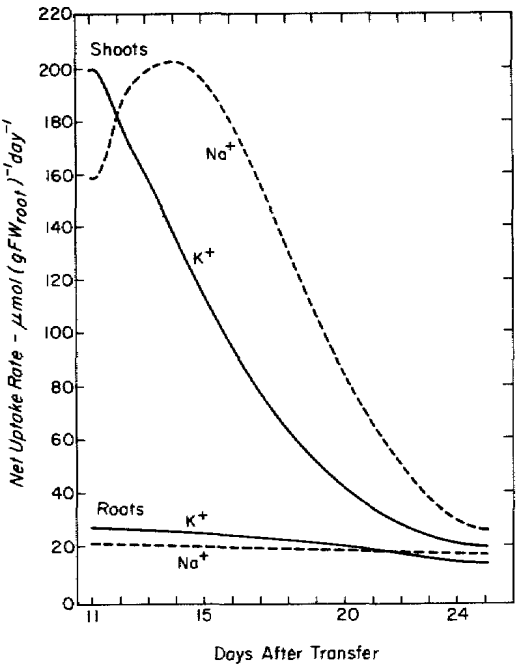

Fig. 5. Net uptake rates (NUR) for Na^+ and K^+ for roots and shoots of mid-vegetative *S. marina*. Data are expressed as μmol (g FW_{root})$^{-1}$ day^{-1} for the most straighforward comparison to isotope experiments. Lines were derived from the growth data using the stepwise program of Hunt and Parsons (1981) and the data from the first growth study.

nology and context of short-term transport studies using isotopes, a further transformation of the growth analysis data using eq. (4) was required. Figure 5 shows the results of that transformation with the net rates of Na^+ and K^+ accumulation by roots and leaves of *S. marina* expressed as μmol (g fresh $weight_{root}$)$^{-1}$ day^{-1}.

Conversion to hourly rates required an additional adjustment for diurnal variation. That adjustment was made for Na^+ using the data previously reported for $^{22}Na^+$ transport (Cheeseman and Wickens 1986a). With similar data obtained for $^{42}K^+$ (data not shown), with appropriate attention to the differences in root and shoot patterns, and with the assumption that net uptake and isotope uptake showed similar diurnal variations, the linear rates of isotope uptake (Cheeseman and Wickens 1986b) and "corrected" net daytime uptake are compared in Tab. 3 for plants 17 days after transfer to solution culture.

Table 3 shows an apparent discrepancy between the estimated rates of transport to the shoot, with isotope transport being greater than net transport. This difference was in the direction opposite to that which would be expected if the specific activity of the transporting compartment in the roots were less than the specific activity of the external, isotope-labeled medium (Pitman 1972). Figures 2 and 5 suggest a probable source of the disparity. In spite of the relatively steady internal ion levels and the appearance of a "steady state", the rates of net accumulation were most rapidly changing at this age; the net accumulation rate of either ion in the leaves decreased by ca 30% between days 16 and 18. Root accumulation rates decreased by 9% for K^+ and 3% for Na^+.

With respect to total weight, the plants used in the isotope study were mid-way between the averages for days 16 and 17 in the growth study (Cheeseman and Wickens 1986b). The two estimates in Tab. 3 are, thus, at least in reasonable agreement for leaf accumulation rates. In the roots, on the other hand, isotope and net accumulation results showed poor agreement. Isotope accumulation rates were more than twice that of net uptake and no simple corrections could be applied to reconcile the data. As net uptake was closely associated with growth (Fig. 2), the discrepancy must reflect ion exchange between mature cells and the external medium.

Table 4 shows a comparison of the changes in net and isotope-estimated accumulation rates with age. Because of the disparity of root values (Tab. 3), this comparison

Tab. 3. Comparison of net and labeled K^+ and Na^+ accumulation rates in *S. marina* plants 17 days after transfer to solution culture. Net rates (± SE) were taken from the analyses used for Fig. 5. Uncorrected values are daily rates divided by 24. Isotope rates are linear values (± SE) reported previously (Cheeseman and Wickens 1986b). Correction factors (CF) are based on 2 h $^{42}K^+$ and $^{22}Na^+$ accumulation studies and are the ratios of the daytime (08 00 to 18 00 h) to 24 h average rates (Cheeseman and Wickens 1986a). All rates are μmol g FW_{root}^{-1} h^{-1}.

Part	Ion	NUR uncorrected	CF	NUR corrected	Isotope uptake
Shoot	K^+	3.24±0.06	1.68	5.44	6.05±0.33
	Na^+	6.50±0.11	1.35	8.78	10.7±0.8
Root	K^+	0.95±0.01	1.30	1.24	2.69±0.14
	Na^+	0.80±0.01	1.24	0.99	2.53±0.21

Tab. 4. Comparison of net and labeled K^+ and Na^+ accumulation rates in the leaves of mid-vegetative *S. marina* plants growing on 0.2× sea water medium. Net rates are from the study shown in Fig. 5. Isotope rates are linear rates in time course experiments at each age.

Age days	% of day 17			
	NUR		Isotope uptake	
	K^+	Na^+	K^+	Na^+
15	147	125	110	189
17	100	100	100	100
19	65	67	22	61
21	44	42	14	38

was limited to leaf accumulation. Relative net uptake rates were determined using the results in Fig. 5. Isotope results are from a separate study performed in December 1984. Again the results showed reasonable agreement of the two estimation techniques. It is noteworthy that the changes in isotope accumulation rates in roots were similar to those in the leaves. This suggest an age-dependent change in the exchange properties of mature root cells.

Discussion

In this study, we have considered the accumulation of Na^+ and K^+ by mid-vegetative *Spergularia marina* plants with particular attention, first, to the relationship between accumulation and growth, and second, to the comparability of uptake rates estimated using short-term isotope or longer-term net accumulation techniques. Together, these supplement our previous studies using *S. marina*, placing the consideration of transport physiology in the context of the growing, autotrophic plant. Consistent with the previously observed correlations between size, RSR, root K^+ content and isotope uptake (Cheeseman and Wickens 1986b), we have found a decrease in the rate of uptake of both ions with age (Fig. 5). Most notably, the decline in rates of net accumulation correlated with the increase in RSR after day 15 (Fig. 3), and the result of the putative control network was a stabilization of ion content with age (Fig. 2). Preliminary analyses (not shown) of isotope accumulation rates at different ages have indicated that RSR has the most significant correlation to isotope accumulation at all ages, though at present we have insufficient data with respect to root ion concentrations to perform a full statistical analysis.

These results also confirm our conclusion that the growth of *S. marina* is stimulated by NaCl (Cheeseman et al. 1985a). The stimulation was related in part to a substitution of Na^+ for K^+ and to an increase in the efficiency of K^+ utilization (Tab. 1). It would be expected that Na^+ substitutes for K^+ in its osmotic role (Clarkson and Hanson 1980). It is not certain, however, how this results in the positive energy balance required for the plant to increase growth; though our earlier studies have shown that the K^+ uptake system is energy dependent (Cheeseman et al. 1985b), they have also shown that Na^+ is excluded against a substantial electrochemical gradient. Thus, the savings realized by not transporting K^+ must to some degree be lost by the necessity to transport Na^+.

In considering the relationship between ion uptake and growth per se, we have analyzed RGR and RAR. As these are relative measures expressed with the same units ($time^{-1}$), comparison of the results is straightforward. A similar but less robust technique was used by Raper et al. (1977) for a study of tobacco growth. Though their calculations were based on mean values for weights and contents and only 2 harvests, they found a broad agreement between RGR and RAR for several nutrients.

Pitman (1972) also considered the relationship between K^+ accumulation and growth, and reported a correlation between the net rate of K^+ uptake (NUR) and RGR in barley. The calculations were again based on only 2 harvests and were restricted to young seedlings; photoperiod was used to adjust RGR. Pitman's results are not easily considered, in part because the interpretation of that particular linear correlation is not immediately apparent, and in part because the treatments did not simply alter RGR. Complex changes, including differential alteration of root and shoot growth and an overall retardation of the development cycle also occurred, as they did in the growth study used for Fig. 4 of this paper. Here, however, with the comparison based on changes in the relative growth and accumulation rates, the interpretation of the results remains straightforward.

RGR and RAR behaved similarly throughout the two growth studies in spite of discontinuities in the growth conditions in the second study. It is not unreasonable to postulate that the processes of growth and nutrient acquisition are, in fact, co-regulated rather than simply correlated as might be concluded from the results of the first study alone. A similar conclusion follows from the review by Ingestad (1982) which provides an extensive consideration of growth rates and nutrient contents of plants grown on very dilute, but carefully maintained, nutrient media. He showed that in order to maintain constant concentrations in the medium during a period of plant growth, the rate of addition of nutrients to the medium had to increase exponentially. In effect, by analyzing the adjustments of the medium, Ingestad was analyzing RAR under those nutrient limited conditions, and with illustrations taken from his work on *Betula* and *Alnus*, he showed a one-to-one relationship between RGR and RAR (for nitrogen) over the range of about 0.025 to 0.25 day^{-1}.

It is unlikely that the integration of uptake and growth can be explained by any model involving regulation of a single transport system, or even one for each ion. It is still unknown what messengers are actually involved and how they interact with the transport systems themselves. And it is unclear how the transport systems may change in total or specific activity with age. Clearly, these questions are fundamental to understanding the physiology of ion transport in the context of the intact plant and deserve further attention.

For the present, however, these results reaffirm the precept that a unit of balanced growth utilizes a unit of nutrients (Clarkson and Hanson 1980), and show that in *S. marina* Na^+ can be included in the generalization. They are also consistent with, and provide a physiological, short-term basis for investigating the numerous block models which have been developed to discuss plant responses to changes in nutrient availability (e.g. Chapin 1980, Moorby and Besford 1983).

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References

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

Cheeseman, J. M. & Wickens, L. K. 1986a. Control of Na^+ and K^+ transport in *Spergularia marina*. I. Transpiration effects. – Physiol. Plant. 67: 1–6.

– & Wickens, L. K. 1986b. Control of Na^+ and K^+ transport in *Spergularia marina*. II. Effects of plant size, tissue ion contents and root-shoot ratio at moderate salinity. – Physiol. Plant. 67: 7–14.

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

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

Clarkson, D. T. & Hanson, J. B. 1980. The mineral nutrition of higher plants. – Annu. Rev. Plant Physiol. 31: 239–298.

Glass, A. D. M. 1983. Regulation of ion transport. – Annu. Rev. Plant Physiol. 34: 311–326.

Hunt, R. 1982. Plant Growth Curves: The Functional Approach to Plant Growth Analysis. – Edward Arnold Ltd., London. ISBN 0-7131-2844-5.

– & Parsons, I. T. 1981. Plant Growth Analysis: User's Instructions for the Stepwise and Spline Programs. – Unit of Comparative Plant Ecology (National Environment Research Council) University of Sheffield.

Ingestad, T. 1982. Relative addition rate and external concentration; Driving variables used in plant nutrition research. – Plant Cell Environ. 5: 443–453.

Moorby, J. & Besford, R. T. 1983. Mineral nutrition and growth. – *In* Encyclopedia of Plant Physiology, New Series (A. Läuchli and R. L. Bieleski, eds), Vol. 15B, pp. 481–527. Springer-Verlag, Berlin. ISBN 0-387-12103-X.

Nye, P. H. & Tinker, P. B. 1969. The concept of a root demand coefficient. – J. Appl. Ecol. 6: 293–300.

Pitman, M. G. 1972. Uptake and transport of ions in barley seedlings. III. Correlation between transport to the shoot and relative growth rate. – Aust. J. Biol. Sci. 25: 905–919.

Raper, C. D. Jr., Patterson, D. T., Parsons, L. R. & Kramer, P. J. 1977. Relative growth and nutrient accumulation rates for tobacco. – Plant Soil 46: 473–486.

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