Salinity tolerance in *Spergularia marina*

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Attributes of the coastal halophyte *Spergularia marina* (L.) Griseb. that make it useful for studies of the physiological basis for salt tolerance in fully autotrophic higher plants are discussed. Growth, morphological, and ion-content characteristics are presented to serve as a background for subsequent studies of transport physiology. Plants were grown in solution culture on dilutions of artificial seawater or on the same solution without NaCl ("fresh water") from the time at which they could be conveniently transferred as seedlings (about 2 weeks old) to the onset of flowering about 5 weeks later. Eighteen days after transfer, plants growing on 0.2× seawater were larger, being nearly twice the size of plants on fresh water. A Na^+ specific effect was indicated, as the major part of the growth stimulation (54%) resulted from a 1 m*M* NaCl supplementation of "fresh water." Succulence was not a consideration in the growth response: root length was directly proportional to weight as was leaf surface area and neither was affected by salinity. Total Na^+ plus K^+ per gram root or shoot showed little variation with salinity from 1 to 180 m*M* Na^+ levels. In roots, the relative Na^+ and K^+ contents were also little affected by salinity, but in the shoots, increasing salinity resulted in higher Na^+ and lower K^+ contents. Distribution within the shoots of 0.2× plants showed no regions either free of or exceptionally high in Na^+. The ion content and distribution patterns are compared with those in a number of other halophytes.

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Des caractéristiques de l'halophyte *Spergularia marina* (L.) Griseb. rendant cette plante utile dans les études sur les bases physiologiques de la tolérance aux sels des plantes supérieures complètement autotrophes sont discutées. Des données sur la croissance, la morphologie et la teneur en ions sont présentées en vue de servir de fondement à des recherches subséquentes sur la translocation. Les plantes furent cultivées en solutions nutritives additionnées de diverses dilutions d'eau de mer artificielle ou en solution nutritive sans NaCl ("eau fraîche"), à partir du moment convenable à leur transfert (à l'âge d'environ 2 semaines), jusqu'au début de la floraison, environ 5 semaines plus tard. Dix-huit jours après le transfert, les plantes croissant sur la solution d'eau de mer diluée 0.2× avaient une dimension près du double de celles du traitement eau fraîche. L'apport d'1 m*M* de NaCl a causé une stimulation de croissance (54%), et cet effet est attribuable spécifiquement à Na^+. La succulence n'a pas été prise en considération dans l'étude de la croissance: la longueur des racines était directement proportionnelle au poids, de même la surface foliaire, et ni l'une ni l'autre n'a été affectée par la salinité. Les teneurs totales en Na^+ et en K^+ par gramme de racine ou de tige ont montré peu de variation avec des niveaux de salinité de 1 à 180 m*M* de Na^+. Dans les racines, les teneurs relatives en Na^+ et K^+ furent aussi peu affectées par la salinité, mais dans les tiges, l'augmentation de salinité a résulté en des teneurs plus élevées en Na^+ et plus faibles en K^+. La distribution du sodium dans les tiges des plantes du traitement 0.2× eau de mer n'a pas montré de régions soit libres, ou soit exceptionnellement élevées en Na^+. La teneur en ions et leurs patrons de distribution se comparent à ceux de nombreuses autres halophytes.

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Introduction

It is well established that salinity tolerance in higher plants is not the result of pronounced differences in tolerance at the enzyme level (Flowers et al. 1977; Greenway and Munns 1980; Munns et al. 1983). Thus it is at least arguable that our understanding of salt tolerance and its variations could be advanced by consideration of transport processes throughout the plant, of their integration, and of their control. Detailed consideration of transport at the plant level is, however, hampered by the difficulties imposed by plant size on, for example, analysis of radioisotope content. Cultural limitations, especially in regard to light, also raise doubts about the significance of results. It is, therefore, worthwhile and appropriate at this time to consider the use of species which might be particularly suited to available culture and analytical techniques.

In this paper we describe some of the characteristics of *Spergularia marina* which indicate that it is suitable for such studies, particularly when small size, culturability, and a high degree of salinity tolerance are desirable. We emphasize those growth and physiological characteristics that establish a background for subsequent reports on specific aspects of transport physiology.

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Materials and methods

Plant culture

Plants were grown in solution cultures in artificial seawater, modified as previously described (Johanson and Cheeseman 1983) to include nitrogen, phosphorus, and micronutrients. "Fresh water" designates 1/10-strength seawater excluding NaCl, and "1/1" designates the freshwater medium (1 m*M* K^+) supplemented with 1 m*M* NaCl. Plants were grown in continuously aerated solution culture in a growth chamber maintained at 22:15°C (day:night), with a 14-h photoperiod. There was no control over relative humidity, which varied widely with season. Lighting consisted of a bank of fluorescent tubes (Westinghouse F96T12/D/SHO); irradiance at plant height was approximately 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Seeds were germinated on vermiculite watered with 0.6× medium (excluding NaCl). Distilled water was added daily to keep the vermiculite wet. During the germination period, plants were kept on a light bench at a photon flux density of approximately 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Seedlings were transferred to solution culture at various ages (but constant for a species) as determined largely by their ability to survive the transfer. Roots were inserted through holes in 1 cm thick Styrofoam supports floating on freshwater medium in 28 × 40 × 5 cm plastic trays. Each support island contained 162 plants (one species per tray) spaced on an 18 × 25 mm grid unless otherwise stated. Cultures were maintained at reduced light for 5 days then transferred to the full light conditions described above. Salinization, if any, began 7 days after transplanting, proceeding through

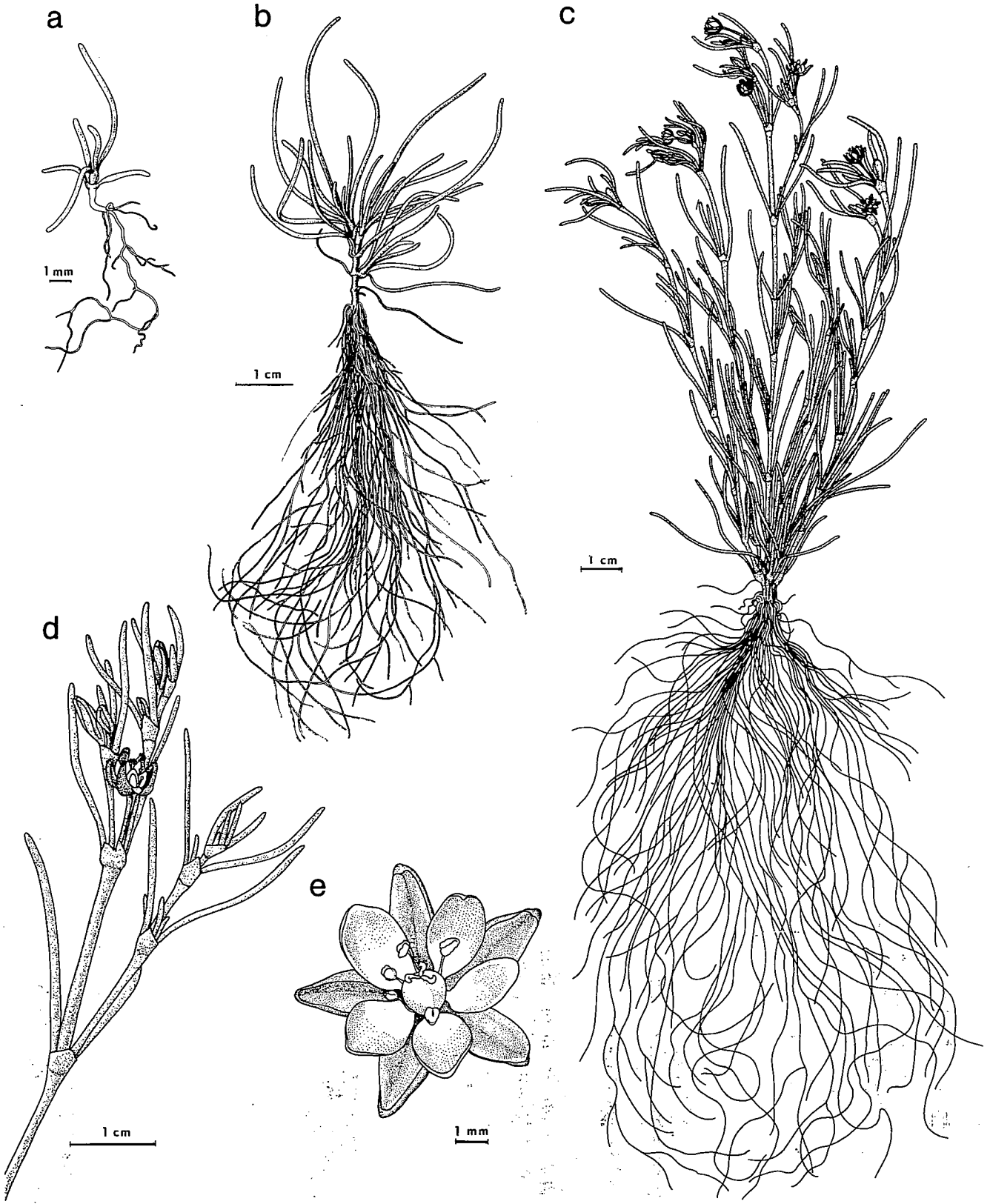

FIG. 1. *Spergularia marina* plants drawn from life, using growth-chamber plants. (*a*) Seedling at time of transfer to solution culture. (*b*) Midvegetative plant 18 days after transfer. (*c*) Reproductive plant at onset of flowering, approximately 35 days after transfer. (*d* and *e*) Details of plant at onset of flowering.

the sequence 0.1×, 0.2×, 0.4× seawater at daily intervals. K^+ levels were measured by flame photometry every other day and were restored to the original with KNO_3. All solutions were replaced at weekly intervals.

Plant material

Aster tripolium L. seeds were collected from the rocks at Garbh Leac, Isle of Gigha, Argyll, Scotland, in August 1983. Seedlings were transferred to solution culture when they had two to four leaves. The

TABLE 1. The effect of growth-medium salinity on root (W_r), leaf (W_l), and total plant fresh weight (W_p) and on root:shoot ratio (RSR) in *Spergularia marina* at 18 days after transfer to solution culture

Growth medium*	W_r	W_l	W_p	RSR
Fresh water	0.066±0.004	0.189±0.009	0.270±0.013	0.302±0.009
Seawater				
0.1×	0.076±0.005	0.235±0.007	0.329±0.011	0.287±0.012
0.2×	0.105±0.003	0.400±0.011	0.527±0.014	0.260±0.004
0.4×	0.090±0.003	0.327±0.008	0.434±0.010	0.293±0.008

NOTE: Weight of the root–shoot interface is included with the leaves for calculation of RSR. Data are means ± SEM, $n \geq 110$.

*"Fresh water" is 1/10-strength modified artificial seawater excluding NaCl but containing 1 m*M* K^+. Seawater is appropriately diluted modified seawater (see Johanson and Cheeseman 1983).

number of studies using this species was limited by uneven germination and by lack of a local seed source.

Seeds of *Lycopersicon cheesmanii* ssp. *minor* (Hook.) C. H. Mull, Galapagos coastal ecotype 1401, were obtained from Professor E. Epstein of the University of California, Davis. Plants were grown for seed in the departmental greenhouses, and that seed was used in all experiments. Seedlings were transplanted at the cotyledon stage. Survival in solution culture required that cotyledons and leaves remained away from the Styrofoam surface and were dry at all times.

Plantago maritima L. seeds were collected from various saline sites, with numerous differences in leaf and growth form between populations. For the present experiments, the original seed source was at the end of the jetty, Ardminish, Isle of Gigha. Mature leaves of plants from this population were erect, up to 20 cm long and approximately 0.8 cm wide at midlength.

Plantago arborescens Poir. seeds were collected from plants in the departmental collection. Seeds were originally obtained from the Institut Botanic, Barcelona, Spain. The ultimate source of the seeds was an unknown location in the Canary Islands.

Puccinellia maritima (Huds.) Parl. seeds were collected in July 1983 in the salt marsh on Bull Island, Dublin, Eire. Transfer to solution culture was after several leaves had formed and the plants were approximately 20 cm high. Lack of seed limited use of this species.

Spergularia marina (L.) Griseb. seeds were collected at Kincardine Bridge, Scotland, in October 1979 as an inadvertent addition to plant samples of other species. Seeds which germinated in the greenhouse at Stirling University were grown to seed and transferred to the collection at the University of Illinois in 1980. Seeds from the progeny of a single plant have been used in these experiments.

Zea mays L. ((A632 × Crows 3640) × Oh 43, Crows Hybrid Corn Co., Milford, IL) was germinated on moist paper towels in the dark and transferred to solution culture and to the light 3 days later. Instead of the shallower containers used for other species, 2-L black Plexiglas boxes, 14 cm deep, were used. Ten plants were grown in each box.

Analytical techniques

At harvesting, roots were rinsed in two changes of ice-cold 20 m*M* $CaCl_2$, for a total time of 10–15 min. Aerial parts were rinsed briefly in a similar solution. For analysis, plants were divided into roots, root–shoot interface, and leaves. Plants were weighed, dried, reweighed, and ashed at 500–525°C for 3 h. Ashed samples were resuspended in 1 *M* magnesium acetate at a ratio of approximately 0.1 g dry weight per millilitre. Samples were shaken briefly on a Vortex mixer approximately 15 min prior to analysis. Na^+ and K^+ contents were determined by flame emission spectroscopy (Instrumentation Laboratories, model 643).

Root lengths were determined by the method of Tennant (1975) using a 4.2-mm grid spacing. Leaf surface areas were measured using a LiCor model LI-3000 area meter; reported values are twice the measured, single-surface areas. Root diameters were measured with a calibrated micrometer eyepiece. Relative contributions of taproots and secondary and tertiary roots to the total system were estimated from the numbers and lengths of different root types in the microscope field at low magnification.

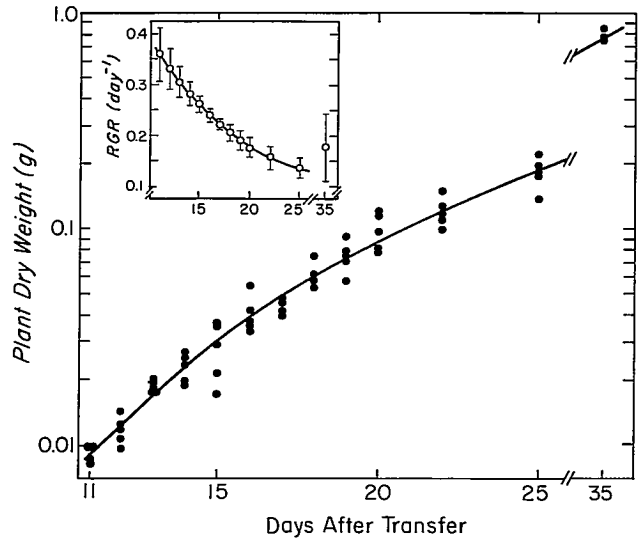

FIG. 2. Total dry weight of *Spergularia marina* plants as a function of time after transfer to 0.2× modified artificial seawater. The frequent small harvest method of Hunt (1982) was used. Points represent individual measurements. Line was fitted using the program of Hunt and Parsons (1981). Inset, RGR with 95% confidence limits calculated using the same program.

Growth analysis was based on small frequent harvests (Hunt 1982) and data were analyzed using the stepwise method of Hunt and Parsons (1981).

Results

Spergularia marina seeds began germinating within 2 weeks of spreading on vermiculite and seedlings were transferred to solution culture approximately 2 weeks thereafter (Fig. 1*a*). The seedlings grew rapidly, reaching the size shown in Fig. 1*b* approximately 18 days after transfer. At this "midvegetative" stage, just before elongation of branches, the plants were nearing a minimum in their relative growth rates (RGR) (Fig. 2). This RGR was high both in comparison with agronomic plants and with other halophytes (Munns et al. 1983), though Yeo and Flowers (1980) have reported a value nearly as high for another annual but highly succulent halophyte, *Suaeda maritima*. Leaf dimensions of fully expanded leaves and root morphology in *S. marina* were similar to those of the reproductive plants. Figure 1*c* shows the plant approximately 5 weeks after transfer to solution culture, at the onset of flowering. Figures 1*d* and 1*e* show details of plants at that age. Though the

TABLE 2. The size and contribution of different root types to the total root system in *Spergularia marina* plants 2–3 weeks after transfer to solution culture

Root type	Diameter (μm)	Estimated proportion of total root system
Taproot	312±21	0.1
Secondary	199±5	0.7
Tertiary	151±5	0.2
Weighted average	200	

NOTE: There was no significant difference between estimates made on plants grown on fresh water (1/10-strength modified artificial seawater without NaCl) and plants grown on 0.2× modified artificial seawater.

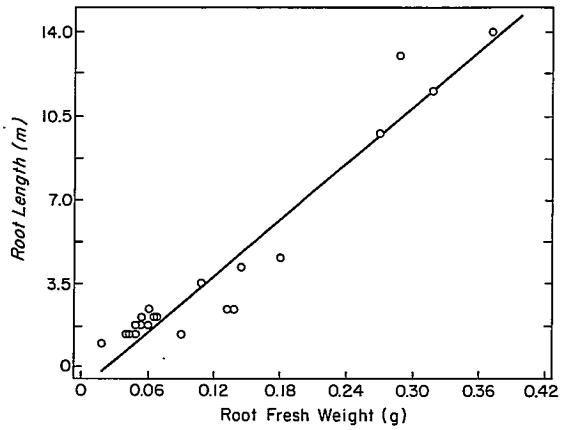

FIG. 3. The relationship between root length and root weight in *S. marina* plants grown on fresh water. Solid line determined by linear regression using all points: $L = 38.7 \cdot W_r - 0.73$; $r = 0.964$.

time of first flowering was advanced slightly at higher salinity, beginning at 38 days on freshwater medium and at 34 days on 0.2× seawater, the difference was probably of little significance; flowering was indeterminate and flowers were autogamous. Branching and flowering, with gradual loss of aging leaves, continued for some months and was accompanied by copious seed production.

The effect of salinity on plant size at 18 days after transfer to solution culture is shown in Table 1. Both root and shoot weights were greatest at 0.2× seawater and were substantially above fresh water levels at 0.4× seawater. The greater fresh weight of 0.2× plants was maintained at least to the onset of flowering, at which time it was 140% of the freshwater value.

In a separate experiment, addition of 1 m*M* NaCl to the freshwater medium ("1/1") resulted in a 54% increase in total plant fresh weight from 0.60 to 0.93 g per plant ($n = 10$; SEM = 0.05) at day 14 after transfer. The increased growth over the freshwater value resulting from inclusion of this non-saline level of NaCl was similar to the Na^+ stimulation of sugar beet growth reported by El Shiekh et al. (1967).

Though root weight is usually the most conveniently determined root size parameter, length or surface area might sometimes be more logically connected with transport activity. As indicated in Fig. 1, however, there was little variation in root size between secondary and tertiary roots in *S. marina*. Table 2 shows the distribution of root sizes and their relative proportions of the total root system. Total root length was proportional to root fresh weight (Fig. 3). With the exception of the taproot, diameters were constant for several centimetres back from the tips. The taproot was somewhat greater in diameter, especially in the basal centimetre, but represented a small portion of the total root system. Calculated root surface area was, thus, also linearly related to root fresh weight, being 2.4×10^{-2} m^2 g^{-1}. Inclusion of root hairs (estimated at 6×10^4 per metre with an average length and diameter of 5×10^{-4} and 9.4×10^{-6} m, respectively) increased the total estimated surface to 6×10^{-2} m^2 g^{-1}. The relationship between surface area and root weight was also estimated by the methylene blue method of Sattelmacher et al. (1983). Exchangeable dye was a linear function of root weight ($r = 0.90$).

Measured leaf surface area was linearly related to shoot weight at least up to day 22, prior to marked branch extension. The relationship was similar for plants grown on freshwater and

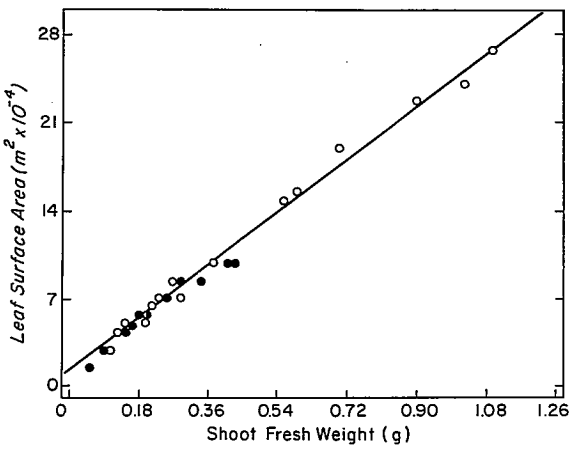

FIG. 4. The relationship between leaf surface area (two surface values) and shoot weight in midvegetative *Spergularia marina* plants grown on fresh water (●) and 0.2× modified artificial seawater (○). Line determined by linear regression: area = 0.00235 · W_l + 0.00009; $r = 0.996$.

TABLE 3. The effect of growth medium salinity on root and leaf Na^+ and K^+ concentrations in midvegetative *Spergularia marina* plants

Growth medium*	Ion	Ion content (μmol/g fresh weight) Roots	Leaves
Fresh water	Na^+	1.1±0.3	6.7±0.4
	K^+	103±2	140±4
	Na^+/K^+	0.01	0.05
Supplemented fresh water	Na^+	52±3	49±1
	K^+	97±7	194±3
	Na^+/K^+	0.54	0.25
Seawater			
0.1×	Na^+	88±3	106±5
	K^+	92±3	153±9
	Na^+/K^+	0.96	0.73
0.2×	Na^+	86±1	166±4
	K^+	82±2	103±5
	Na^+/K^+	1.1	1.6
0.4×	Na^+	85±4	185±9
	K^+	102±9	88±2
	Na^+/K^+	0.86	2.1

NOTE: Data are for plants 2 weeks after transfer to solution culture.

*Fresh water is 1/10-strength modified artificial seawater excluding NaCl but containing 1 m*M* K^+. Supplemented fresh water ("1/1" medium) is 1/10-strength modified artificial seawater containing 1 m*M* K^+ and 1 m*M* NaCl. Seawater is appropriately diluted modified artificial seawater (see Johanson and Cheeseman 1983).

TABLE 4. A comparison of shoot Na^+ and K^+ concentrations (micromoles per gram fresh weight) in *Spergularia marina*, *Zea mays*, and five other relatively tolerant species considered as potentially useful experimental systems

Growth medium*	Ion	*S. marina*	*Plantago maritima*	*Plantago arborescens*	*Lycopersicon cheesmanii*	*Aster tripoleum*	*Puccinellia maritima*	*Zea mays*
Fresh water	Na^+	6.7	1.6	1.1	<1	<1	<1	<1
	K^+	140	179	94	48	140	118	119
	Na^+/K^+	0.05	0.01	0.01	—	—	—	—
Supplemented fresh water	Na^+	49	14	4.2	—	—	—	—
	K^+	194	164	87	—	—	—	—
	Na^+/K^+	0.25	0.09	0.05	—	—	—	—
Seawater								
0.2×	Na^+	166	236	240	92	110	77	98
	K^+	103	72	107	60	104	159	129
	Na^+/K^+	1.6	3.2	2.3	1.5	1.1	0.48	1.3
0.4×	Na^+	185	280	—	191	—	—	—
	K^+	88	57	—	62	—	—	—
	Na^+/K^+	21	5.0	—	3.1	—	—	—

NOTE: Data are for plants 2 weeks after transfer to solution culture.
*Fresh water is 1/10-strength modified artificial seawater excluding NaCl but containing 1 m*M* K^+. Supplemented fresh water ("1/1" medium) is 1/10-strength modified artificial seawater containing 1 m*M* K^+ and 1 m*M* NaCl. Seawater is appropriately diluted modified artificial seawater (see Johanson and Cheeseman 1983).

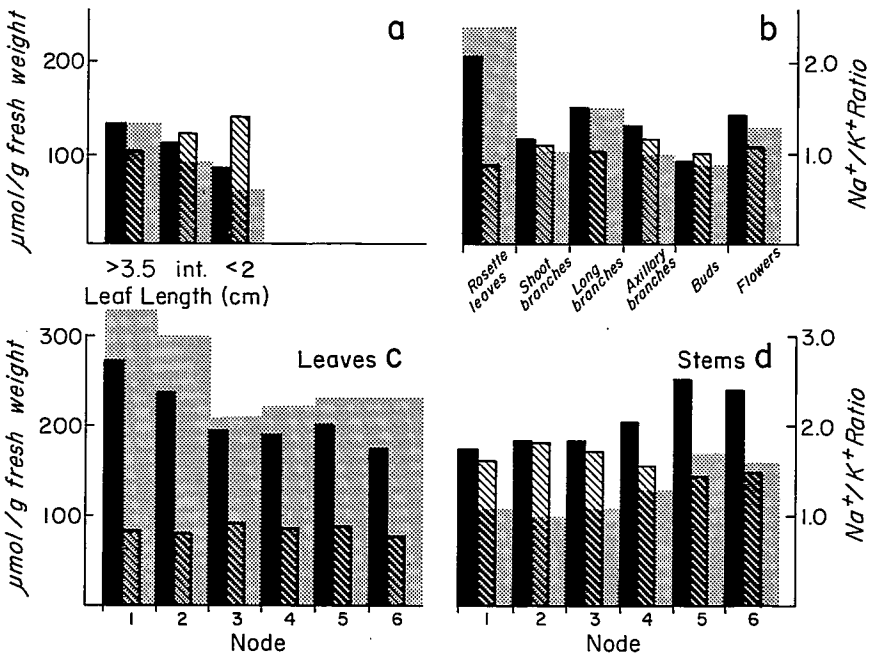

FIG. 5. The distribution of Na^+ (solid bars), K^+ (hatched bars), and the Na^+/K^+ ratio (stippled) in *Spergularia marina* shoots in midvegetative plants separated by leaf length (*a*) and at the onset of flowering. (*b*) Distributions within parts of the shoot at onset of flowering. (*c*) Distributions in leaves separated by node in six-node branches numbered from the base. (*d*) Distributions in stem sections basal to each leaf pair in Fig. 5*c*. "int." designates intermediate leaf lengths.

0.2× seawater media (Fig. 4).

The Na^+ and K^+ contents and their ratios in roots and shoots of *S. marina* at the midvegetative stage are shown in Table 3. On 0.1× to 0.4× media, the total Na^+ plus K^+ content showed little variation in either roots or shoots and was only slightly lower in plants grown on freshwater medium supplemented with 1 m*M* NaCl. The latter growth conditions resulted in a significant increase in total monovalent cation and shoot K^+ contents. In the roots of plants grown on dilutions of complete seawater, the relative proportions of Na^+ and K^+ were also constant. In the shoot, the constant $Na^+ + K^+$ was accompanied by an increase of Na^+ and a decrease of K^+.

Table 4 compares these results with the shoot contents of several other species grown under similar conditions in the growth chamber. In *Plantago maritima*, K^+ content was more sensitive to salinity than it was in *S. marina*. *Plantago arborescens* was similar to *Plantago maritima*. Though neither showed growth reduction on 0.2× seawater, *Plantago arborescens* did not survive transfer to 0.4× seawater. *Lycopersicon cheesmanii* had a lower K^+ content in freshwater medium but no decrease with increasing salinities, despite a large reduction in growth (Rush and Epstein 1976, 1981). *Puccinellia maritima* showed Na^+ exclusion similar to that of corn but without elevated Na^+ levels at the base of the shoot.

Growth was not reduced at 0.2× seawater. *Aster tripolium* behaved more like the monocots than the dicots, maintaining a low Na^+/K^+ ratio at 0.2× seawater. Unlike the other species, K^+ concentrations were higher in the roots than in the shoots (data not shown). *Aster tripolium* in solution culture developed a second, adventitious root system with much thicker and sparsely branched roots. This system, not seen in soil-grown plants, may have different nutrient transport properties than the normal root.

The Na^+/K^+ ratio shown here for *Aster tripolium* at 0.2× seawater is much lower than the field values reported for plants in Welsh salt marshes by Gorham et al. (1980), as might be explained, in part, by the fact that these plants were both younger and growing at much lower salinities. A field value similar to theirs ($Na^+/K^+ = 7.8$) was found in *A. tripolium* collected in the Kincardine Bridge and Bull Island salt marshes in the summer of 1983 and in *Plantago maritima* and *Spergularia media* (8.5 and 13.2, respectively). However, the field value for Na^+/K^+ for *S. marina* at full seawater salinity was only 4.5. Thus the Na^+-exclusion ability at high Na^+ suggested by the growth-chamber experiments is not inconsistent with field results.

Figure 5 shows the distribution of Na^+ and K^+ within the shoots of plants grown on 0.2× seawater at two different stages, midvegetative (as shown in Fig. 1*b*) and at the onset of flowering (as in Fig. 1*c*). In the younger plants (Fig. 5*a*) Na^+ was highest in the older leaves; K^+ mirrored Na^+ so that the Na^+/K^+ ratio was lowest in the younger leaves. At flowering, the basal leaves had the highest Na^+ levels and the highest Na^+/K^+ ratios. Short branches (one or two nodes) and axillary shoots off the longer branches had lower levels of Na^+, and the longer branches (three to seven nodes) had intermediate levels.

Figures 5*c* and 5*d* detail the distributions along six-node branches. The ion ratio varied with length, largely because of a lower Na^+ content in the younger tissue. Both flowers and flower buds contained significant amounts of Na^+ and had Na^+/K^+ ratios close to unity. This latter characteristic also contrasts with the data for *Aster tripolium* presented by Gorham et al. (1980).

Discussion

In this paper we have considered the characteristics of several halophytes which relate to their usefulness in studies of salt transport and tolerance in wild plants. Of the species considered, we found *Spergularia marina* to be the most tractable as an experiment organism.

Spergularia marina, a coastal halophyte occurring throughout Britain and Europe and found also in North America, until now has received little attention as a possible experimental plant. Other than one report from this laboratory (Cheeseman and Enkoji 1984), it has been the subject of germination studies by Ungar (1984) and Okusanya and Ungar (1983). Gorham et al. (1980) have reported that *S. marina* accumulated proline but not quaternary ammonium compounds under saline conditions and this was confirmed recently by Stumpf (1984).

There are several characteristics of *S. marina* which make it a desirable experimental subject. First, at the site of our original seed collection it is subject to relatively small fluctuations in daily temperature in the growing season and to frequent overcast days. Our growth-chamber conditions are, thus, less unrealistic than they might be for many plants. Second, *S. marina* is an annual with a short life cycle; thus data relevant to any stage in the cycle can be obtained easily and without the complications of perennials. Third, the growth response to salinity is such that interpretation of results at different salinities can be made without consideration of changes in growth form or succulence.

With the spacings of plants used in these experiments, shoots of midvegetative plants were nonoverlapping, though root systems were intertwined. *Spergularia marina*, however, showed none of the root brittleness associated, for example, with *L. cheesmanii*. On the contrary, the root systems could be separated easily by gentle manipulation. This manageability continued even into the flowering stage, and for the drawing of Fig. 1, gentle agitation of the plants in a shallow dish produced the separation illustrated.

Finally, the vegetative plants are small. Therefore, *S. marina* is useful for isotope studies well into the vegetative stage.

Further studies will consider the uptake and transport mechanisms involved in salinity tolerance in *S. marina* and their relationship with growth and energy metabolism in fully autotrophic plants.

Acknowledgements

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