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Physiology of halophytes

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Summary The cellular basis of salt tolerance in halophytes depends upon the compartmentation of ions necessary for osmoregulation in vacuoles and upon osmotic adjustment of the cytoplasm by compatible solutes. The central role played by Na^+ and Cl^- in osmotic adjustment suggests that the transport of these ions and its regulation must be of primary importance in the physiology of the plant as a whole. There have been few investigations into the regulation of leaf ion concentrations, but such data as are in the literature suggest that limiting xylem Na^+ (and Cl^-) concentrations, together with continued leaf expansion, are particularly important. The role of phloem in retranslocation is uncertain due to lack of data. Decreases in transpiration rate per unit area of leaf help to lower the ion input into leaves. Any linked reductions in photosynthesis appear to be due to decreases in stomatal frequency.

Introduction

As a result of research carried out largely during the last decade [17, 35, 51], it has been possible to deduce the essential features of the cellular basis of salt tolerance in higher plants. For members of the Chenopodiaceae at least, the ability to withstand high external salt concentrations appears to depend on osmotic adjustment, most commonly with Na^+ and Cl^-, but since these are toxic their concentration in the cytoplasm is maintained substantially lower than in the vacuoles (Table 1). Osmotic adjustment in the cytoplasm is achieved with compatible organic solutes [44, 46]. This brief summary of a number of years of experimental work is necessarily neglectful of detail, but highlights the central role played by sodium and chloride in the physiology of the dicotyledonous halophytes. It is their ability to cope with high internal concentrations of Na^+ and Cl^- that separates halophytes from glycophytes. This brief review will then be concentrated on our knowledge of ion transport from root to leaf and its regulation and involvement in growth; often there will be more questions than answers.

Terminology

Plants grown at a constant external NaCl concentration over a period of weeks are considered to be in a 'steady state' in order to contrast them with those recently (up to a few days) subjected to a change in the external salinity.

Table 1. Ion distribution in mesophyll cells of mature leaves of *Suaeda maritima* (L.) Dum. grown at a steady-state salinity of 340 m*M*

Cell compartment	Vol[a] per cell (pl)	Concentration[b] ($mol\,m^{-3}$)			Relative contents[f]		
		Na^+	K^+	Cl^-	Na^+	K^+	Cl^-
Cytoplasm	9.2	116(136)[c]	19(21)[c]	60(71)[c]	0.03	0.10	0.02
Chloroplasts	1.2	104(208)[d]	22(44)[d]	98(196)[d]	0.003	0.02	0.004
Mitochondria	0.6	–	–	–	–	–	–
Vacuole	67.8	494	20	352	0.94	0.84	0.95
Cell wall	4.4	194(554)[e]	14(40)[c]	138(394)[e]	0.02	0.03	0.02
Total	83.1				35.5[f]	1.6[f]	25.1[f]

a. Data of Hajibagheri[24]
b. Data of Harvey *et al.*[28] : the concentration is in $mol\,m^{-3}$ of analyzed volume and not $mol\,m^{-3}$ H_2O.
c. Value in parenthesis assumes 85% (v/v) water content.
d. Value in parenthesis assumes a 55% solute-available space – (ref. [37], p. 86).
e. Based on the water content (35%, w/w) of filter paper at – 1.5 MPa (ref. [50]).
f. Relative to the total content in pmol.
– No data available.

Osmotic adjustment

It has long been known that halophyte cells must have lower water potentials within than outside the plasmalemma to retain cellular water and that the necessary osmotic adjustment in dicotyledons is largely achieved by Na and Cl ions[16]. In the Gramineae, however, K^+ and sugars appear to aid in fulfilling this role[1,20]. The use of organic compounds as vacuolar solutes in succulent halophytes seems to be precluded on energetic grounds[56]. Thus, in succulent halophytes, vacuolar concentrations (based on tissue water) of Na^+ and Cl^- generally exceed the external concentrations, and by a considerable margin where the latter are low (Table 2). This appears to reflect a constitutive ability of halophytes to accumulate high ion concentrations [17]. However, although steady-state Na and Cl ion contents, expressed per unit dry weight, of leaves of some species appear to be relatively constant over higher external NaCl concentrations [16], this is not necessarily so if the leaf concentration is based on the water content. It is, however, very difficult to make any general conclusions concerning the regulation of these ion concentrations (see[11]), because of a lack of information on plant water potential, turgor and ion fluxes.

There is still a dearth of data on ion transport and on net ion fluxes to the shoots of halophytes, largely because too few investigators record data with time[35]. For *Suaeda maritima* plants growing in the

Table 2. The effect of changed external salinity (Na_{out}) on Na and Cl ion concentrations (m*M*) in the leaves (Na_{vac}, Cl_{vac}) of various halophytes

Species and family	Na_{out}	Na_{vac}	$\frac{Na_{vac}}{Na_{out}}$	Cl_{vac}	$\frac{Cl_{vac}}{Cl_{out}}$	Reference
Atriplex nummularia	50	348	7.0	314	6.3	4
Chenopodiaceae	200	429	2.1	338	1.7	
	600	870	1.4	834	2.1	
A. nummularia	10	538[a]	[b]	189	19	22
Chenopodiaceae	100	618[a]	6.2	252	2.5	
	300	751[a]	2.5	483	1.6	
A. hastata	100	658	6.6	430	4.3	7
Chenopodiaceae	400	1203	3.0	911	2.3	
A. spongiosa	50	114	2.3	37	0.74	47
Chenopodiaceae	500	598	1.2	341	0.68	
Suaeda maritima	170	380	2.2			54
Chenopodiaceae	340	450	1.3			
S. monoica	50	695	14	392	7.8	47
Chenopodiaceae	500	843	1.7	624	1.2	
Jaumea carnosa	155	166	1.1	162	1.0	45
Asteraceae	600	496	0.83	340	0.57	
Avicennia marina	49	456	9.3	306	5.3[c]	14
Avicenniaceae	123	550	3.7	362	2.5[d]	
	493	956	1.9	631	0.92[e]	
Disphyma australe	25	101	4	80	3.2	36
Aizoaceae	100	222	2.2	157	1.6	
	500	475	0.95	364	0.73	
Elymus oliveri[f]	75	140	1.9			2
Poaceae	100	169	0.56			
Puccinellia maritima[f]	100	112	1.1			2
Poaceae	400	139	0.35			

a, Na^+ plus K^+; b, meaningless; c, $Cl_{out} = 58$ m*M*; d, $Cl_{out} = 145$ m*M*; e, $Cl_{out} = 580$ m*M*; f, unaerated culture but see ref. [10].

steady state in 340 m*M* NaCl, net sodium fluxes to the shoot during the growth of the plant range between 5 and 9 mmol/g dry weight of roots/day and are reasonably correlated with the relative growth rate calculated on the basis of the organic dry weight (Table 3). This net flux is considerably higher than the K^+ fluxes reported for glycophytes (1 to 2 mmol/g d.w. roots/day [39, 40, 56]) and indicates the enhanced transport capabilities of some halophytes as compared with glycophytes. However, for halophytic members of the Graminae, which differ from dicotyledenous plants in terms of net accumulation of Na ions [1, 20] (and Table 2), Na ion fluxes are lower, especially relative to fluxes of K^+ (Table 3). Although net K^+ fluxes are rather low in Suaeda (*cf.* 39),

Table 3. Relative growth rates (RGR) and net ion fluxes (J) to the shoots of three salt-tolerant species. The relative growth rates of Suaeda are based on organic dry matter alone

Species	t (days)	J_{Na} (mmol/g d.w. root/d)	J_K (mmol/g d.w. root/d)	RGR (d^{-1})	J_{Na}/J_K	Reference
Suaeda maritima (340 m*M*)	21–28	6.21	0.65	0.174	9.6	54
	28–35	9.44	0.86	0.249	11.0	
	35–42	8.04	0.55	0.169	14.6	
	42–49	5.09	0.21	0.116	24.2	
	21–49	7.20	0.57	0.177	14.9	
Elymus oliveri (150 m*M*)	3–33	0.48	0.51	0.10	0.94	2
Puccinellia maritima (200 m*M*)	7–63	0.30	0.34	0.10	0.88	2

there may be considerable retranslocation of K^+ from older leaves to the shoots[55], which thus maintain adequate K/Na ratios in the rapidly growing apices[21].

Potassium is evidently required during initiation of protein synthesis, and in most cells cytoplasmic concentrations seem to be about 80–100 m*M*[52]. In mesophyll cells of *S. maritima*, the K^+ concentration is estimated to be only about 20 m*M* (Table 1). This low concentration may be characteristic of mature cells, where Na^+ may substitute for K^+ (see 18), while higher K^+ concentrations exist in meristemic zones [21]. It is, however, apparent from preliminary results in our laboratory that Suaeda microsomes in a heterologous *in vitro* protein synthesis system with wheat postribosomal supernatant are more tolerant of low K^+ and high Na^+ than are wheat ribosomes themselves and can incorporate methionine at 70% of maximal levels (*i.e.* with 120 m*M* potassium acetate) in the presence of 120 m*M* Na^+ and 28 m*M* K^+. The extent to which Na^+ may substitute for K^+ in protein synthesis remains to be fully explored.

For plants growing under natural conditions, rapid osmotic adjustment is presumably essential to cope with fluctuations in the external osmotic potential brought about by rain and drought. It has been calculated from measurements of the initial influx of radioactive ions into *S. maritima* that osmotic adjustment to seawater salinity can be achieved in 24–48 h[17, 56]. In young plants (32d) an increase in the external NaCl concentration from 2 or 200 m*M* to 202 and 400 m*M*, respectively, increased net transport to the shoot to maximum rates of 9 and 11 mmol/g dry weight root/day, respectively, some 6 h after the increase in salinity [9]. Levels of abscisic acid in the shoot also increased over a 24-h period, approximately doubling for plants going from 0 to 200 m*M* NaCl and increasing five-fold when the salinity was increased

Table 4. Salt concentration in a variety of saline environments

Site	Range Na (m*M*)	Reference
Salt marsh, Hudson Bay, Canada	100–1060	32
Salt marsh, Stiffkey, U.K.	200–910	31
Salt marsh, Georgia, U.S.A.	262–710*	3
Salt marsh, New South Wales, Australia	283–593*	8
Salt desert, Utah, U.S.A.	217–2380*	27
Mangrove swamp, New South Wales, Australia	289–808*	8

*Calculated assuming water with a salinity of 35% has an osmotic pressure of 2.60 MPa, that Na is 30.4% of the S% and that the specific gravity is measured at 25°C to a maximum level of 1.025, (ref. [29]). Chloride concentration would be about 15% higher.

from 200 to 400 m*M* [9]. It appears unlikely, however, that halophytes have to cope with high water potentials, since dilution of the external solution to produce an osmotic potential greater than — 1.0 MPa seems to be uncommon, from the minimum sodium concentrations recorded in various saline marshes (Table 4). Halophytes are therefore presumably adapted to tolerate fluctuations in the external salinity following rain and drought, but with a minimum Na^+ concentration of about 200 m*M* (or perhaps 100 m*M*). A low internal osmotic potential presumably obviates the need for continuous osmotic adjustment under fluctuating salinities and presumably aids the maintenance of positive turgor.

Until recently it has been difficult to estimate turgor pressure in the cells of halophytes. Data on osmotic potentials are relatively easy to obtain and closely reflect changes in the Na^+ and Cl^- concentrations, decreasing with increasing external salinity [16, 17]. This is so not only in whole plants, but in individual leaves [9]. However, good water potential measurements are most difficult to obtain. Those made on excized leaves are probably unreliable because of the high concentrations of salt in cut cells and in cell walls (Table 1). Low water permeabilities make the use of whole leaves in psychometers equally questionable because of excessive equilibration times. Furthermore, the very low water potentials mean very high pressures are required if a pressure bomb is used, and little or no exudate is attainable [42]. However, use of a pressure probe in Wyn Jones' laboratory has shown that turgor is maintained approximately constant in mature leaves of Suaeda at various external salinities [48] (and Fig. 1). Since vacuolar concentrations of Na^+ and Cl^- vary considerably under these conditions, this suggests that a turgor homeostat may operate as outlined by Cram [11]. Even in

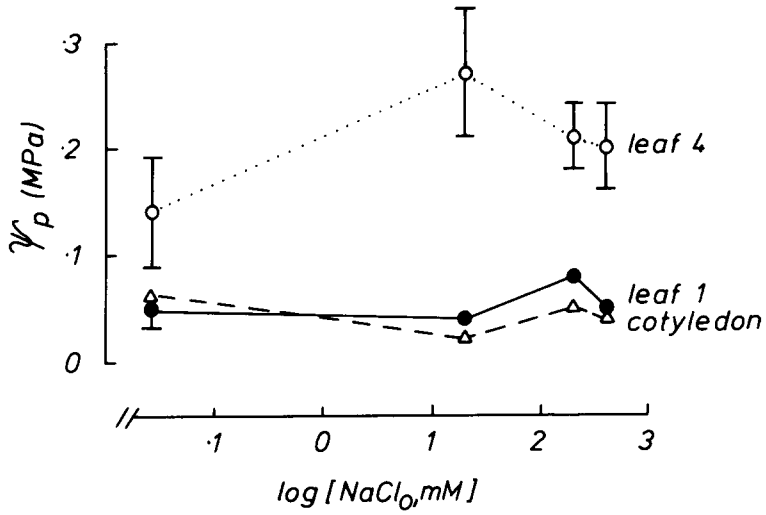

Fig. 1. The turgor pressure in leaf epidermal cells of 27 to 29 day old plants of *Suaeda maritima* grown at various steady-state salinities (mean ± standard deviation). Where no error bar is shown the deviation was too small to illustrate. Leaf age decreases with increasing number. Unpublished data of Clipson and Tomos.

younger leaves (leaf 4), where turgor pressure may reach 0.4 MPa, the variation in turgor is small (less than 0.15 MPa) over a wide range of external salinities (about 1 MPa – Fig. 1).

Factors affecting leaf ion concentrations

In principle, regulation of vacuolar ion concentrations with time, at a steady-state external salinity, could be achieved through balancing import (xylem), export (phloem or salt-glands where present), and volume (i.e. water content). There have, however, been few investigations on the long-term balance of ion concentration within individual leaves. Leaf expansion in Rhizophora, a mangrove species without salt glands, continued throughout the life of the leaf, and the water content per leaf increased with leaf age[5] (and Fig. 2). The amount of sodium per leaf also increased, but its concentration did not change in older leaves. An increase in the fresh weight per leaf was also reported for *Mesembryanthemum crystallinum* grown for over 28 days under saline conditions, although a continuing increase in weight did not occur in older leaves [53] (and Fig. 2). A similar picture appears to hold for leaves of *Suaeda maritima*, although measurements were made over a shorter period (Fig. 2). It is also apparent from work with a pressure probe [48] that the elastic modulus of walls of Suaeda leaves declined with

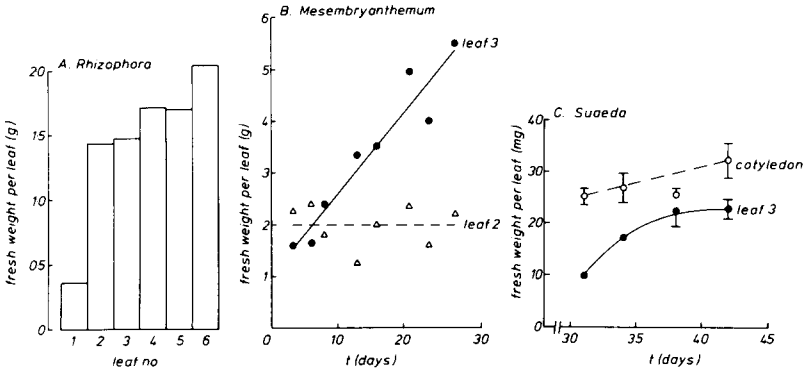

Fig. 2. Changes in leaf size with time for plants growing under saline conditions. **A.** Rhizophora: leaf 1 is the youngest and leaf 6 beginning to senesce. Drawn from the data of Atkinson et al.[5]. **B.** *Mesembryanthemum crystallinum*: leaf 2 is older than leaf 3. Redrawn from [53]. **C.** *Suaeda maritima*; unpublished data of the authors. Mean ± s.e.m. After day 35 the number of live cotyledons decreases.

declining turgor. This suggests that in older leaves with lower turgor pressure, continued leaf expansion by uptake of water would have less effect on that turgor pressure than in younger leaves. If the pattern of leaf expansion described above holds for other species then it may be important to distinguish between phases of rapid and then slow expansion in volume, perhaps with increasing and then constant ion concentrations, respectively. However, definitive statements must await studies of leaf volume in relation to leaf age. The maintenance, with time, of constant leaf Na^+ and Cl^- concentrations is evidently much simplified by the presence of salt glands, and species with such glands may tolerate higher salt concentrations in the xylem than those without glands [35]. Thus, although there is too little data for confident generalization, there is a hint that leaf ion concentrations do increase during the early life of a leaf on a plant growing under steady-state salinity [5, 9, 53]. Volume expansion may occur throughout the life of the leaf, albeit at a changing rate. These factors probably play a significant role in the ion relations during the life of a leaf. What may be particularly important as far as the regulation of turgor pressure is concerned is the balance between ion concentations in vacuole and apoplast. As yet, we can only hypothesize.

The delivery of ions to a leaf is a function of the salt concentration in the xylem and the transpiration rate of that leaf. Ion concentrations in the xylem are perhaps best deduced from changes in the shoot ion contents with time and the transpiration rate of intact plants, since detaching shoots from roots dramatically alters the pressure within

Table 5. Na^+ concentration in xylem of several halophytes

	Glands	$[Na]_{out}$ (m*M*)	$[Na]_{xyl}$ (m*M*)	$\frac{[Na]_{xyl}}{[Na]_{out}}$ (%)	Reference
Glaux maritima	+	200	11.6	5.8	41
Armeria maritima	+	200	8.7	4.4	41
Limonium vulgare	+	200	12.2	6.1	41
Spartina anglica	+	200	11.2	5.6	41
Juncus maritima	—	200	7.7	3.9	41
Atriplex litoralis	—	200	5.3	2.7	41
Suaeda maritima	—	200	46.6	23	9
Salicornia virginica	—	210	9.6	4.6	38
S. virginica	—	530	19.0	3.6	38

the xylem (perhaps by some 2.0 MPa for a plant growing in seawater [23]). A large change in pressure is likely to have an effect on ion fluxes [11, 58]. Xylem concentrations of Na^+ calculated from changes in the shoot content range from about 3 to 10% of the external salinity (Table 5). Although higher concentrations have been reported [23, 42], such high values may be suspect if obtained by the use of pressure, which, when applied to cut shoots [41] and roots [43], may result in values higher than those estimated from the ion and water fluxes. However, measurement of the transpiration rates through weighing or other indirect methods (see 5) may also be subject to considerable technical errors. In a recent study, Na ion flux in *Suaeda maritima*, a halophyte without glands, was deduced from both tracer fluxes and changes in shoot ion content. Transpiration was measured by gas exchange[9]. Xylem concentrations of Na^+ calculated from net transport agreed well with those based on tracer fluxes and varied with the external concentration (Fig. 3); under optimum conditions for growth, Na^+ was about 25% of the external salt concentration (200 m*M*). A particularly notable feature was the apparent increase in xylem Na^+ concentration at night (Fig. 3). However, water fluxes were very low in the dark, and a 10% change in the plant water content would decrease the apparent xylem concentration by about half. An increase in apoplastic water content would be expected if xylem tensions were reduced during the night [57]. This might lessen the apoplastic salt concentration (Table 1) and hence increase cell turgor.

As already mentioned, the delivery of ions to the shoot is a function of the xylem ion concentrations and the transpiration rate. For many years it has been appreciated that the transpiration decreases as the external steady-state salinity increases. However, as with many other aspects of halophyte physiology, the basis on which the transpiration rate is expressed is all important, since salinity affects fresh and dry

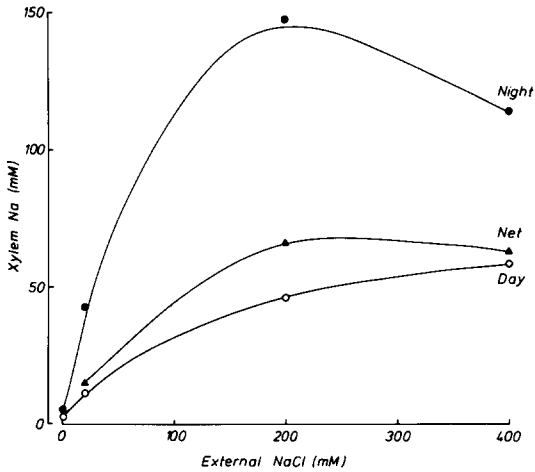

Fig. 3. The effect of steady-state salinity on the xylem concentration of Na^+ calculated from $^{22}Na^+$ transport (●, ○, night and day) and change in shoot ion content (▲). Transpiration rates were measured by gas exchange[9].

weight as well as succulence. It appears that transpiration rates expressed per unit area are depressed at least in the Chenopodiaceae (Fig. 4). For *Suaeda maritima*, the decrease in transpiration is associated with an increase in both stomatal and cuticular resistance (Fig. 5). The increase in cuticular resistance is accompanied by a

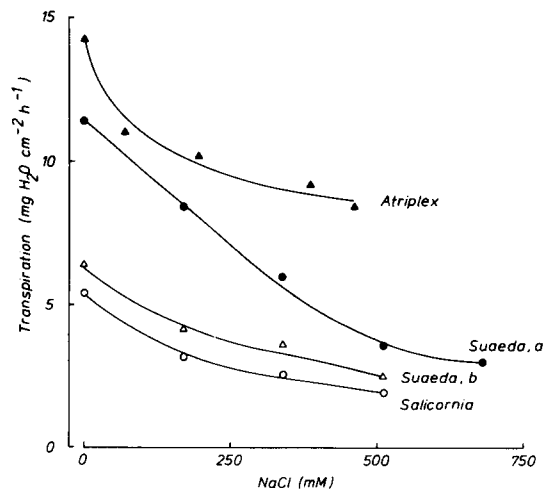

Fig. 4. The effect of increasing steady-state salinity on transpiration in three halophytic members of the Chenopodiaceae. *Atriplex halimus*, saturation deficit (s.d.) 2.5 KPa (drawn from the data in ref. [19]); *Suaeda maritima* (a), s.d. 1.8 KPa (ref. [43]); *Suaeda maritima*, (b), s.d. 0.9 KPa (ref. [13]); *Salicornia europaea* s.d. 0.9 KPa (ref. [13]).

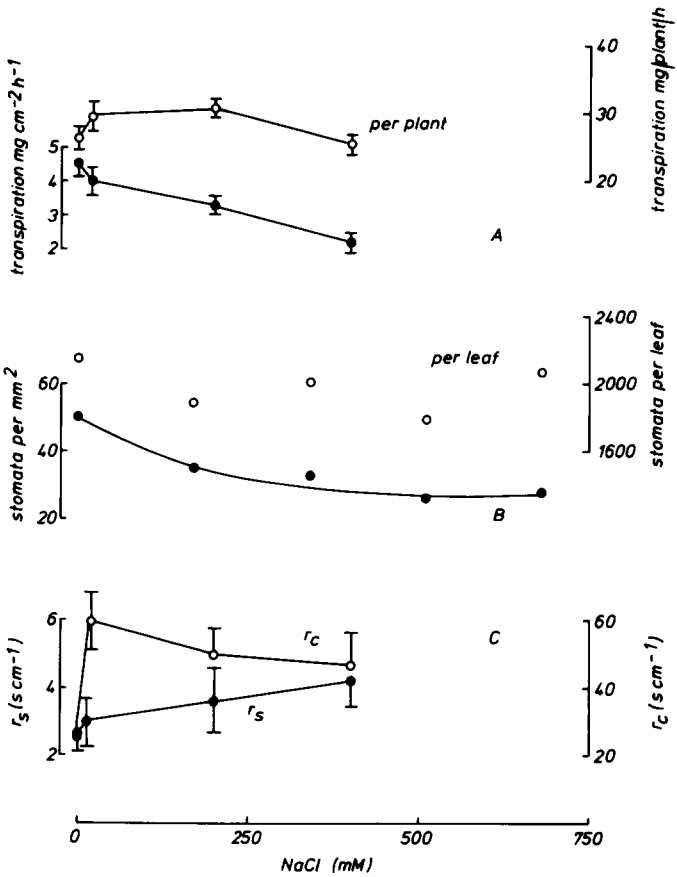

Fig. 5. Transpiration in *Suaeda maritima* at various steady-state salinities. A. Transpiration rates [9] expressed per unit area (•) or per plant (○). B. Stomatal frequencies[43], per unit area (•) or per unit leaf (○). C. Stomatal (•) and cuticular (○) resistances[9]. Vertical bars are standard errors.

1.6-fold increase in the thickness of the cuticle and a 1.8-fold increase in that of the epidermal cell wall under saline conditions, together with a change in the appearance of the epicuticular wax [25]. The change in stomatal resistance parallels exactly a change in stomatal frequency and so does not necessarily imply any increase in resistance to movement through the stomata themselves. Changes in stomatal frequency are, in fact, a consequence of the increase in succulence and have been reported for Salicornia [13] and Distichlis[33]. In *Suaeda maritima* then, transpiration per plant increases under saline conditions (Fig. 5) as a consequence of an increased leaf area. However, ions delivered per unit area or per unit volume of leaf will be reduced, probably as a consequence of the reduced stomatal frequency. Although many general features of the

water relations have been deduced, there is still insufficient data to determine the effects of leaf age on water flux and ion balance. Such experiments would now be very timely. Furthermore, the extent of possible differences in transpiration rates between leaves are unknown, as is the extent of bypass flow in halophytes.

There are indications from an anatomical study that the development of the Casparian strip occurs within 3 mm of the root tip in *Suaeda maritima* plants grown under saline conditions and is retarded in the absence of NaCl: 15 mm from the root tip the Casparian strip averages 0.93 μm in length in salt-grown plants but only 0.46 μm in plants raised in nonsaline culture solution [24]. Vacuolation of epidermal and cortical cells is also enhanced by salinity. Although root development is not remarkably more rapid than in salt-resistance glycophytes (see ref. [35], p. 111), early prevention of apoplastic flow would assist in controlling the amount of ions in the shoots. Another feature of *S. maritima* roots is the narrow width of the cortex (3 cells), a feature previously noted in other halophytes [48]. It has been speculated [23] that this may play a role in minimizing ion concentration gradients across the endodermis. However, the model on which these conclusions were based did not specifically include ion uptake by the root, and the true significance of the narrow cortex in these plants must await further work.

There is almost no information concerning phloem Na^+ (and Cl^-) concentrations in halophytes[23] and the possible rates of export of these ions from leaves. Calculations based on the cross-sectional area of phloem in *S. maritima* leaves indicate that Na^+ export from a mature Suaeda leaf might approach 20% of daily import, assuming a phloem Na^+ concentration of 30 m*M*. However, Yeo[55] established that there was little if any apical movement of Na ions from mature leaves of Suaeda into new leaves, a point neglected by Greenway and Munns[23]. The importance of K^+ retranslocation in maintaining adequate K/Na ratios has already been discussed.

The effect of salinity on transpiration per unit area indicates that concomitant effects on photosynthesis may be expected. Such changes may be important in understanding the effects of salinity on growth, in particular, the inhibition of growth at high salinity. Again, determination of the true effect of salinity on the photosynthetic rate is liable to be confounded by the basis of expression, since salinity treatment affects fresh and dry weight and leaf area. Rates per unit area are decreased or are little affected by NaCl. Although there are very few data available, rates per unit of chlorophyll appear either to be unaffected or to increase (Table 6) with increasing external salinity. There is, therefore, little evidence to suggest any major effects of

Table 6. The effect of external salinity (steady state) on net photosynthesis (P_N) expressed per unit area and per unit of chlorophyll in several halophytes. Data are expressed as percent of non-saline controls

Species	$NaCl_{out}$ (m*M*)	P_N(%)		Reference
		per area	per chlorophyll	
Distichlis spicata	250	71	–	33
	500	60	–	
Aeluropus litorolis	100	–	93	15
Aster tripolium	85	125	–	6
	170	114	–	
	340	98	–	
Atriplex halimus	68	89	–	19
	195	93	–	
	462	64	–	
Suaeda maritima	100	–	125	51
	400	–	125	
	20	90	92	9
	200	80	100	
	400	72	103	

salinity on photosynthesis *per se*, and *in vitro* electron transport from water to ferricyanide is notably tolerant of high Cl^- [12, 26]. There does not appear to be evidence to suggest a decline in photosynthesis *per se* as the cause of growth inhibition at high salinity.

Conclusions

Growth data on halophytes are difficult to evaluate, since such a high proportion of the dry weight consists of ions. Although it is easy to subtract these and compute data on a organic dry matter basis, when there is little stimulation of growth[38, 54] the usefulness of this subtraction in evaluating growth and its costs depends upon whether a significant proportion of energy is required for salt transport. The costs of salt transport were considered in some depth in two recent reviews [23, 56]. The consensus is that at high salinities ion transport (through cost or capacity) may limit osmotic adjustment and hence limit growth, presumably through loss of turgor. The rather low turgor pressures recorded for *Suaeda maritima* (Fig. 1) suggest that ion accumulation in cell walls (Table 1) may be an important element of the ion relations in a leaf. Decrease in growth and in leaf longevity at high salinity may be determined by this ion accumulation. It is clear from the number of unknowns entering into the calculations of Yeo[56] and of Greenway and Munns[23] that further attempts at evaluating the energetics of ion

transport might be more fruitful if based on an analysis of the carbon and energy budgets, given the problems with the measurement of chemical potential gradients. Such an approach might evaluate the sources of energy for osmotic adjustment – whether photosynthetic or respiratory. It is interesting to note in this respect that large parenchyma cells surrounding the vascular bundles in mature leaves of *Suaeda maritima* contain very few mitochondria and no chloroplasts[24] and may rely on electrical coupling to mesophyll cells for ion transport. It is also noteworthy that chloroplasts of *S. maritima* accumulate starch under optimum growth conditions[24]. Whether this is a consequence of reduced translocation, perhaps induced through phosphate or nitrate deficiency, or simply implies that photosynthesis outstrips demand, is not clear.

An important question relative to this conference is whether the growth rates of halophytes are so low as to preclude their use as crop species. Again, there is rather limited data in the literature on which to base any conclusion, since in most experiments plants are harvested at a fixed time. Certainly the data for Suaeda (Table 3) at its growth optimum do not suggest that the relative growth rates are dramatically limited by salinity, since the maximum value (0.25 day^{-1}; Table 3) is in the range reported for crop species that are not halophytes (0.03 to 0.38 d^{-1})[30]. Long-term values based on organic dry weight (0.18 day^{-1} Table 3, 0.06 g day^{-1} for *Salicornia virginica* [38]) also fall within the range normally reported for glycophytes[30]. It is my view at present, that halophytes do offer a viable alternative[34]. At high salinities their growth is presumably limited not by a single factor but by factors that include a lack of transport capacity, an inbalance in nutrient uptake (*e.g.* K^+, P_i), a limitation on retranslocation of K^+ to growing tips, and excessive ion accumulation in the cell walls of the leaves, which reduces turgor and hence growth. It is clear that the time is right for more detailed experiments aimed at elucidating the regulation of leaf ion concentrations and the overall energy budget of halophytes.

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