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BRIEF COMMUNICATION

SODIUM CONCENTRATION IN XYLEM SAP IN RELATION TO ION EXCLUSION, ACCUMULATION AND SECRETION IN HALOPHYTES

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Salt secretion, salt accumulation and transpiration were simultaneously measured in salt-secreting and non-salt-secreting halophytes and glycophytes. The sodium content of the xylem sap was calculated. It is concluded that salt-secreting halophytes differ considerably in their sodium secretion rates, but less in their sodium exclusion capacity. Salt-sensitivity of the non-secreting species was related to a comparatively high sodium xylem content (15.1 mM Na). Transpiration rates are remarkably similar for all species. It is argued that the distinction between salt accumulators and salt excluders is not only based on differences in ion exclusion but is also related to the capacity to accumulate compatible osmotic solutes.

In experiments aiming at an ecophysiological comparison of the mineral and water economy in relation to halophyte zonation, secretion, accumulation of sodium and transpiration were simultaneously measured in four salt-secreting and four non-salt-secreting halophytes and glycophytes. Plants were grown in a greenhouse (20 °C, 65% RH; 6–18 hr light 7000Lux) in 0.25 strength Hoagland's solution with 0.2 M NaCl added. Salt secretion was measured by rinsing the leaves with distilled water over a 6 day period. Relative humidity of the air was kept at 65% in order to avoid the loss of secreted salt through run-off from the leaves, which occurs under more humid conditions (ROZEMA & RIPHAGEN 1977). Transpiration rates were determined by weight measurement for a 48 hr period. The total weight of the plants which were precultured for four weeks on NaCl-free 0.25 strength Hoagland increased only slightly during the 6 day period. After harvesting and drying, the sodium content of the whole plant was determined by flame emission spectrophotometry. The sodium content of the xylem sap was calculated from the equation:

$$\text{ion concentration xylem sap} = \frac{\text{secretion} + \text{accumulation}}{\text{transpiration}}$$

The results are summarized in *table 1*, and it may be concluded that even the glycophytic species *Juncus articulatus* has the ability to exclude sodium ions to some extent since the rooting medium concentration (200 mM Na) is ten times reduced. In the non-secreting halophyte *Juncus maritimus* the sodium content of the xylem sap is even a factor 150 lower than that of the culture medium. Obviously the stronger exclusion of sodium ions in *Juncus maritimus* relates to its

Table. 1. Comparison of sodium secretion, sodium accumulation and transpiration rate and the calculated sodium concentration of the xylem sap of plants grown on 0.2 M NaCl. Average values and standard deviation of four replications.

species	secretion rate µmol/mg DW.6 days	accumulation rate µmol/mg DW.6 days	transpiration rate mg H_2O/gshoot FW.min	water content % FW	calculated sodium concentration (mM) in xylem sap
salt-secreting					
Glaux maritima	0.18 ± 0.07	1.9 ± 0.13	2.9 ± 0.16	86 ± 3.2	11.6 ± 3.48
Armeria maritima	0.05 ± 0.03	1.4 ± 0.9	2.7 ± 0.02	86 ± 2.5	8.7 ± 1.92
Limonium vulgare	0.49 ± 0.29	1.5 ± 0.14	3.6 ± 0.30	81 ± 1.8	12.2 ± 3.72
Spartina anglica	0.50 ± 0.21	0.8 ± 0.03	3.3 ± 0.11	75 ± 2.1	11.2 ± 1.85
non-secreting					
Juncus maritimus	–	0.1 ± 0.01	2.9 ± 0.08	70 ± 1.4	1.3 ± 0.51
Juncus articulatus	–	1.7 ± 0.02	3.3 ± 0.14	75 ± 1.7	15.1 ± 4.21
Atriplex hastata	–	1.8 ± 0.02	3.6 ± 0.11	86 ± 3.2	7.7 ± 3.08
Atriplex littoralis	–	2.2 ± 0.16	4.2 ± 0.58	87 ± 2.9	5.3 ± 1.86

halophytic status. The low sodium concentration of all the species implies that "desalination" if seawater, which was first described for mangroves by SCHOLANDER (1968) is not unique but occurs in a much wider group of halophytic species and even in salt-sensitive species. Halophytes and glycophytes differ only in the degree of salt exclusion. Salt exclusion by the roots and reduced transport of sodium chloride to the shoot are not the only causal mechanisms involved in halophytism. The calculated sodium content of xylem sap of all four secreting halophytes is about 10 mM, which is higher than the sodium content of the xylem sap of *Juncus maritimus*, but these interspecific differences are smaller than those for secretion rate. Species of the lower saline zones of salt marshes like *Spartina* and *Limonium* secrete sodium ions 2.5–10 times more rapidly than the upper marsh species *Glaux maritima* and *Armeria maritima*.

Many monocotyledonous halophytes adapt to salinity by reduced uptake of salt ("salt excluders") while halophytic Dicotyledonae, members of the Chenopodiaceae in particular, tend to accumulate salt to high levels ("salt accumulators") (ALBERT & KINZEL 1973, GREENWAY & MUNNS 1980).

In this study it appeared that the sodium content of the xylem sap and the sodium accumulation rate of the *Atriplex* species do not exceed those of the other species investigated. Also, it has been shown that the sensitivity of enzymes to NaCl in halophytes and glycophytes is the same (FLOWERS et al. 1977, ROZEMA 1979). It is possibly the synthesis of compatible, organic solutes such as proline (*Glaux*, *Armeria*), homobetaine (*Limonium*) and glycine betaine (*Spartina*, *Atriplex hastata*, *A. littoralis*) (STEWART et al. 1979), which enables halophytic species to continue salt accumulation to high levels without disturbance of metabolism. The absence of high proline concentrations in *Juncus articulatus* in contrast with *J. maritimus* (ROZEMA 1979) would explain the salt-sensitive status of *J. articulatus*. The prevention of NaCl toxicity and osmotic stress due to these compatible osmotic solutes at high salinity in halophytes is absent in glycophytes, where low salinity levels disturb metabolism and reduce growth.

Attemps were made to check the calculated sodium content of the xylem sap by direct determination of sodium in sap collected from cut shoots placed in a Scholander's pressure bomb. Sodium concentration in this "xylem" sap was found to be at least 5–10 times higher than the calculated values. "Xylem" sap pressed from *Atriplex littoralis* and *A. hastata* grown on 0.2 M NaCl showed a Na content of 29.7 and 47.3 mM respectively. Probably the pressure exerted on the damaged tissue surrounding the cutting surface causes the sap collected to be a mixture of xylem sap, cytoplasm and the content of vacuoles.

There are remarkably few reports on the composition of xylem sap. PATE (1976) calculated the sodium content of xylem sap of *Lupinus albus* (2 mM Na) which is in the same order of magnitude as the calculated values given in this paper. Sodium levels in phloem sap reportedly range 2–12 mM.

Halophytism appears to be related to salt exclusion, salt excretion and to the capacity to synthesize compatible organic solutes, but it should be noted that salt-stimulated growth, which rarely occurs in vascular plants, remains unexplained.

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