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Salinity-Stress and Salt-Recretion in Plants

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1 Abstract

Saline soils are widespread on the globe. In climatically arid regions not only coastal areas but all erosion basins tend to become saline, as well as agricultural fields by irrigation (if without drainage).
Salinity stress is thus a worldwide phenomenon in organisms, espec. in plants. Plants have evolved various adaptations to cope with salinity stress. As an example the special group of salt-recreting plants is discussed here. Their anatomical features (salt-glands or bladder structures) are the basis for recreting salt from the mesophyll out of the leaf or to metabollically isolated vacuoles. The activity of the ecophysiological processes as well as the selectivity to ions is discussed. The adaptation to saline stands is documented also by the occurence of the various halophyte types along the salt gradient in nature, as e.g. at salt lakes. The relative ecological advantages of salt-recreting halophytes are shown.

2 Introduction

Salinity-problems in arid countries are widespread. In many countries a high percentage of arable land exhibits increasingly low yields because of accumulation of salt from low quality river water for irrigation and by high evaporation rates of capillary water from the high phreatic water levels. Thus accumulation of salt during the last half century in many agricultural projects is an increasingly severe problem (RICHARDS et al. 1954, STROGONOV 1964, JONES 1970, POLJAKOFF-MAYBER & GALE 1975, GRAETZ & HOWES 1979, SHAINBERG & SHALHEVET 1984).

To cope with stress needs special adaptations. These adaptations can be mainly structural or functional on various levels or both (LEVITT 1980).

Salinity stress needs a general adaptation to the lowered osmotic potential and special adaptations to the distinct ionic effects of Na and/or Cl (WAISEL 1972, ALBERT 1982).

Plants need water from the soil. This is available only when the osmotic gradient can be maintained (HADAS et al. 1973). Uptake of salty water leads inevitably to increasing salt concentrations in the plant-body. The plasmatic adaptation on the one side and the ecophysiologically efficient recretion on the other side is a precondition or a strategy of one group of plants growing on saline stands. But also other adaptations are known to be efficient to cope with salt-stress. This is especially the typical halo-succulence.

3 Adaptations to Salt-Stress in Halophytes

Higher plants which can grow on soils much higher in salt content than the average soils are termed halophytes. There is no other definition, which might be less weak. Various authors use many different parameters to distinguish halophytes from non-halophytes, but the delimitation is not sharp. The same is true for the various systems in classifying halophytes (WAISEL 1972). The necessity of salt for growth was taken as a parameter for halophyte-types by KREEB (1964).

3.1 Halophyte-types

Since decades various classifications for halophytes were suggested. Certainly the controll mechanisms in plants, which maintain a distinct level of sodium concentration in leaves and shoots is an important factor. According to those mechanisms dominant in specific plant-groups halophyte-types can be distinguished on a rather general scheme (Table 1)

Table 1 : Controll mechanisms in plants for maintaining distinct levels of Sodium and Chloride in leaves and shoots and corresponding halophyte-type using predominantly that mechanism (acc. to WAISEL 1972, BRECKLE 1976, BRECKLE 1990, WALTER & BRECKLE 1991)

mechanisms/strategy	Halophyte-Type	examples/species
selectivity of salt-absorption	(NON-HALOPHYTES)	more or less in all species
leaching of leaves	(NON-HALOPHYTES)	more or less in all species
disposal of older plant parts	GLYKO-, PSEUDO-HALOPHYTES	*Juncus, Zygophyllum*
recretion by roots		common? *Suaeda monoica, Salicornia*
increase in halo-succulence - in stems - in leaves	EU-HALOPHYTES	halo-succulents: - stem-succulents - leaf-succulents
recretion by salt-glands	CRINO-HALOPHYTES: EXO-CRINO-H.	*Cressa, Limonium, Glaux, Frankenia, Tamarix* etc.
recretion by bladder-hair	CRINO-HALOPHYTES: ENDO-CRINO-H.	*Atriplex, Halimione*; some *Mesembryanth.*

In the following we will discuss only those halophytes and their adaptations, which are recreting salt by glands or bladder.

3.1.1 Salt-glands and Bladders

In various separately evolved groups of angiosperms we can find structures for salt-recretion. Some of these structures in other genera of the same taxonomic group may have other functions, as e.g. excretion of essential oils. Thus, in this respect a given specific [illegible] systematic entity, may have changed its function by [illegible] needs, e.g. to cope with salt-stress. In table 2 is given a list [illegible] genera with species able to recrete salt is demonstrated.

Table 2 : **Salt recretion in terrestrial halophytes by salt-glands or bladder structures** (partly from LIPHSCHITZ & WAISEL 1982): **Plant-families and genera with crinohalophytic species**

in italics: mangrove-species;
* : only some species of the genus on saline soils
§ : rarely on saline soils

A. species with salt-glands	
Acanthaceae	*Acanthus*
Avicenniaceae	*Avicennia*
Combretaceae	*Laguncularia*
Convolvulaceae	Cressa, Ipomoea*
Frankeniaceae	Frankenia
Myrsinaceae	*Aegiceras*
Plumbaginaceae	*Aegialitis*, Armeria*, Limonium (Statice), Limoniastrum, Plumbago* etc.
Poaceae	Aeluropus, Distichlis, Spartina
Chloridoideae §	Bouteloua, Buchloe, Chloris, Cynodon, Coelachryum, Crypsis, Dactyloctenium, Dinebra, Eleusine, Enteropogon, Sporobolus, Tetrachne, Tetrapogon
Panicoideae §	Andropogon, Brachiaria, Cenchrus, Chrysopogon, Coix, Dichanthium, Digitaria, Echinochloa, Erianthus, Hyparrhenia, Panicum, Paspalum, Paspalidium, Saccharum, Setaria, Sorghum, Tricholaena
Primulaceae	Glaux
Rhizophoraceae	*Ceriops, Bruguiera*
Scrophulariaceae	Cordylanthus, Castilleja*
Sonneratiaceae	*Sonneratia*
Tamaricaceae	Reaumuria, Tamarix*
B. species with bladder cells	
Aizoaceae (s.l.)	Mesembryanthemum (s.l.) et al.*; §;
Chenopodiaceae	Atriplex (Obione)*, Chenopodium*, Halimione, Salsola, et al.?
Oxalidaceae	Oxalis (?)

3.1.2 Anatomy

Species with salt-glands in the various plant-families have evolved apparently several times independently in higher plants. The anatomical structure is often family-specific.
In Fig. 1 - 4 there are given four examples of such glands with only 2 cells or up to 20 cells. In all glands it is very typical that the gland cells are physiologically very active, with dense cytoplasm and high number of mitochondria. The gland apparatus is seperated from the mesophyll by cutinized cell wall layers and the adjacent cells are dense in plasmodesmic joints.
In all salt glands during dry seasons a concentrated brine is recreted, which at the surface crystalizes. By dew in the morning, or by rain the salts are washed down.

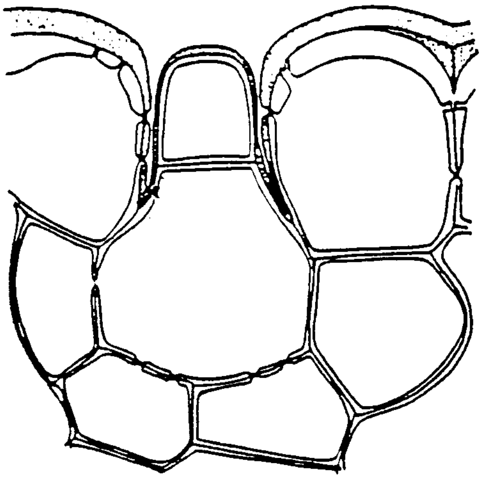

Fig. 1 : Two-cellular saltgland in *Spartina townsendii* (WAISEL 1972)

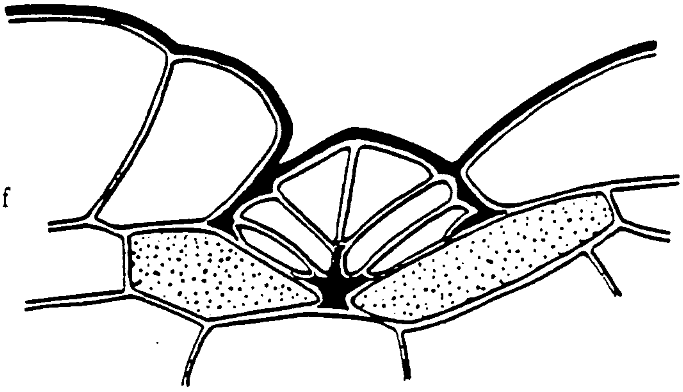

Fig. 2 : Eight-cellular saltgland of *Tamarix aphylla* (WAISEL 1972)

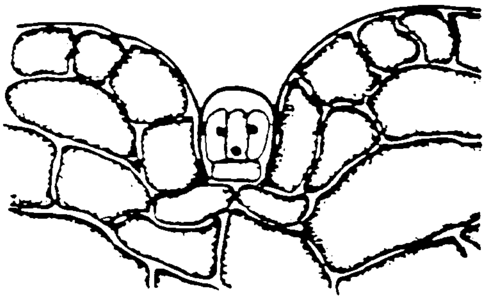

Fig. 3 : Eight-cellular saltgland in *Avicennia marina* (WAISEL 1972)

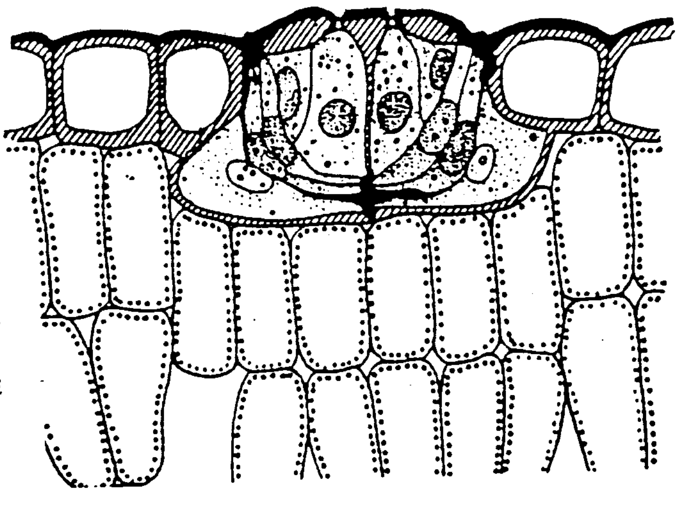

Fig. 4 : Twenty-cellular saltgland in species from the genus *Limonium* (RUHLAND 1915, WIEHE & BRECKLE 1990)

Species with bladders exhibit less variability in bladder structure. In all genera from the Chenopodiaceae the bladder apparatus consists of a large terminal bladder and 1 - 4 stalk cells. The stalk cell(s) function as metabolic active gland cells. They transport brine to the vacuole of the bladder, where it is concentrated and kept inside (Endo-Crino-Halophytes). It is possible that the bladder itself or the whole leaf is seperated and thus the plant has got rid of the salt. In other cases the bladders collapse and form thick mats of salty crusts and cell remnants on the surface. These crusts were originally thought to be the main purpose for that structure in reflecting high sun light radiation. Perennial *Atriplex*-species form continuously new bladder cells, annual *Atriplex* species normally have only one generation of bladders on their leaves.

An extensive study on ecophysiology of *Atriplex* was done by OSMOND et al. (1980), also some of the functions of bladders were tackled.

In Fig. 5 the typical anatomical structure of an C4-leaf (*Atriplex mollis*) from the North-African deserts is shown. This is a perfect example of the bladder cover in these leaves.

In the genus *Chenopodium* also bladders are known. Their structure is similar. In Fig. 6 two different types are shown. In other genera of the Chenopodiaceae such bladder are scercely occuring.

In the Aizoaceae/Mesembryanthemaceae there are some genera which exhibit large bladder cells, too. In this case the enlarged epidermal cells are not so perfectly isolated from the mesophyll as in the Chenopodiaceous bladders. In Fig. 7 the anatomy of epidermal bladder cells from this type is shown.

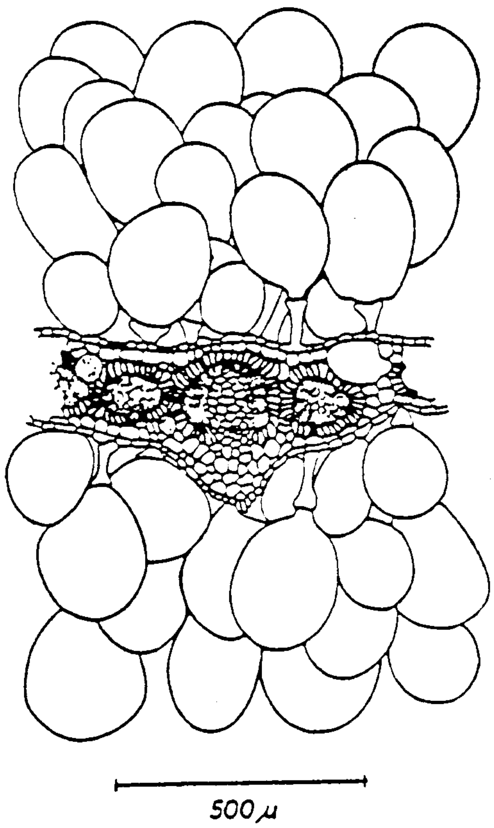

Fig. 5 : Leaf cross-section of *Atriplex mollis* with thick layers of bladder (acc. to BERGER-LANDEFELDT 1959)

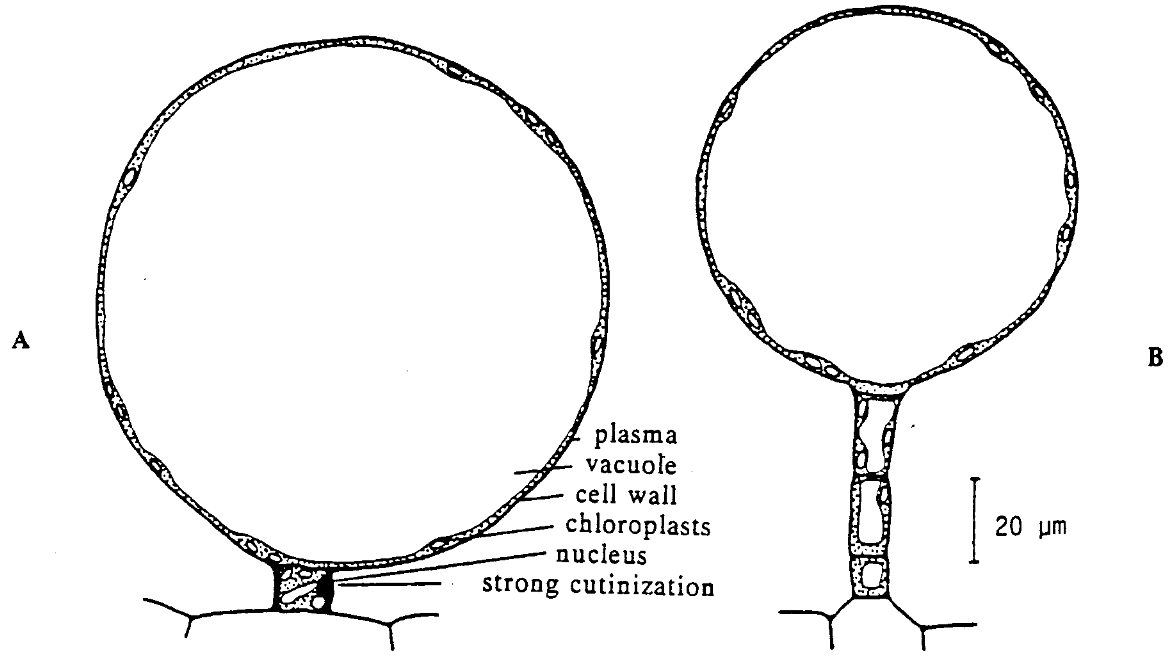

Fig. 6 : Types of bladder in *Chenopodium*. A: *Chenopodium album*, with glandlike structured stalk cell. B: *Chenopodium murale* with several slender, vacuolized stalk cells (REIMANN & BRECKLE 1987)

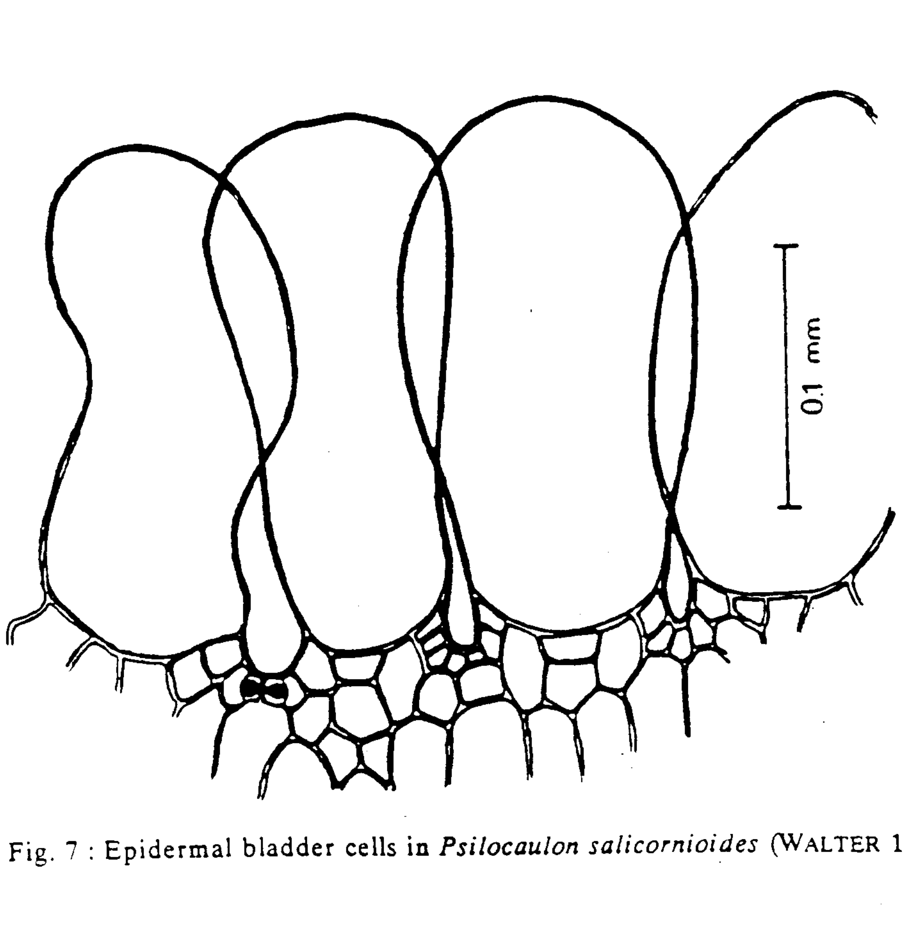

Fig. 7 : Epidermal bladder cells in *Psilocaulon salicornioides* (WALTER 1973)

3.2 Ecophysiological Aspects and Examples

3.2.1 General Remarks

The salt recretion only can be coined effective if the amount of salt within a given time is high enough to keep the salt concentration in photosynthetic active tissues low enough. Of course, this efectiveness is interdependant with many other ecological factors. In *Aeluropus litoralis* by POLLAK & WAISEL already in 1970 it was shown that the salt-concentration in leaves only to some extent can be kept low. Under higher salinities the leaf-concentration increases sharply and the turnover-time also. Thus, to some extent the salt-glands are effective enough but they are not able to cope with very high salt stress (Table 3)

Table 3 : Sodium Recretion and Sodium Content in Leaves from *Aeluropus litoralis* affected by NaCl-Concentration in culture-medium (recalc. from POLLAK & WAISEL 1970)

Na^+ conc. in culture medium [M]	Na+ recreted [μM.mg^{-1}.d^{-1}](d.m.)	Na+ content in leaves [μM.mg^{-1}] (d.m.)	turnover-time [h] to recrete whole Na^+-content
0	0.03	0.17	137
0.005	0.08	0.18	54
0.05	0.19	0.25	32
0.1	0.48	0.43	22
0.2	0.85	0.51	14
0.3	0.99	0.88	21

3.2.2 Salt-glands in *Limonium*

The genus *Limonium* is very widespread in various salty places, along coasts as well as in salt-deserts.
The salt-gland in Limonium is a very complex structure, which was studied in many details from various authors (VOLKENS 1884, LÜTTGE 1971, HILL 1967, ZIEGLER & LÜTTGE 1967). WIEHE & BRECKLE (1990) have demonstrated that the whole apparatus of this salt gland consists of 20 cells and that this structure is rather different in effectiveness in different species. In Fig. 8 the selectivity to Na and K in shoots and salt glands in three *Limonium* species is shown. It is remarkable that the degree of selectivity differs widely. In general the salt glands keep the cytoplasmic mesophyll low in sodium, but much less effective in *Limonium sinuatum*.
A second interesting effect beyond ion selectivity is the fact that the activity of the salt glands apparently is retarded. They only start beyond a specific threshold value of salt concentration in leaves. In Fig. 9 it is clearly indicated that with increasing Cl^--concentration in leaves only beyond 250 μM Cl^- per g H_2O the concentration in the recret fluid is sharply increasing.

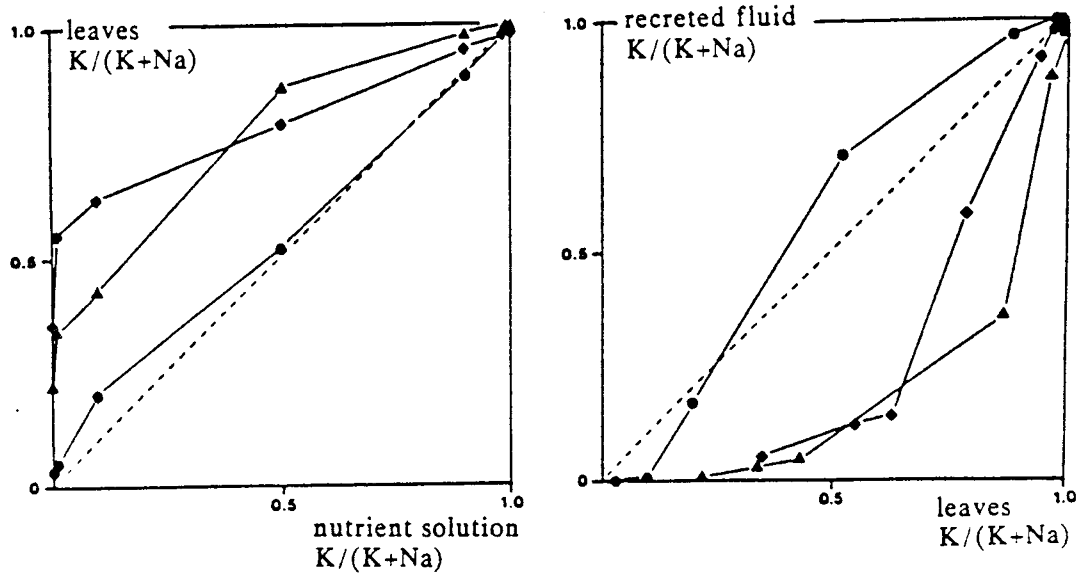

Fig. 8 : Sodium/Potassium selectivity in shoots and saltglands of three *Limonium* species (WIEHE 1986); triangles: *Limonium ramossissimum*; squares: *Limonium gmelinii*; circles: *Limonium sinuatum*; diagonal indicates 1 : 1 - selectivity. Left side: ion ratios from nutrient solution to leaves; right side: ion ratios from leaf to recreted fluid.

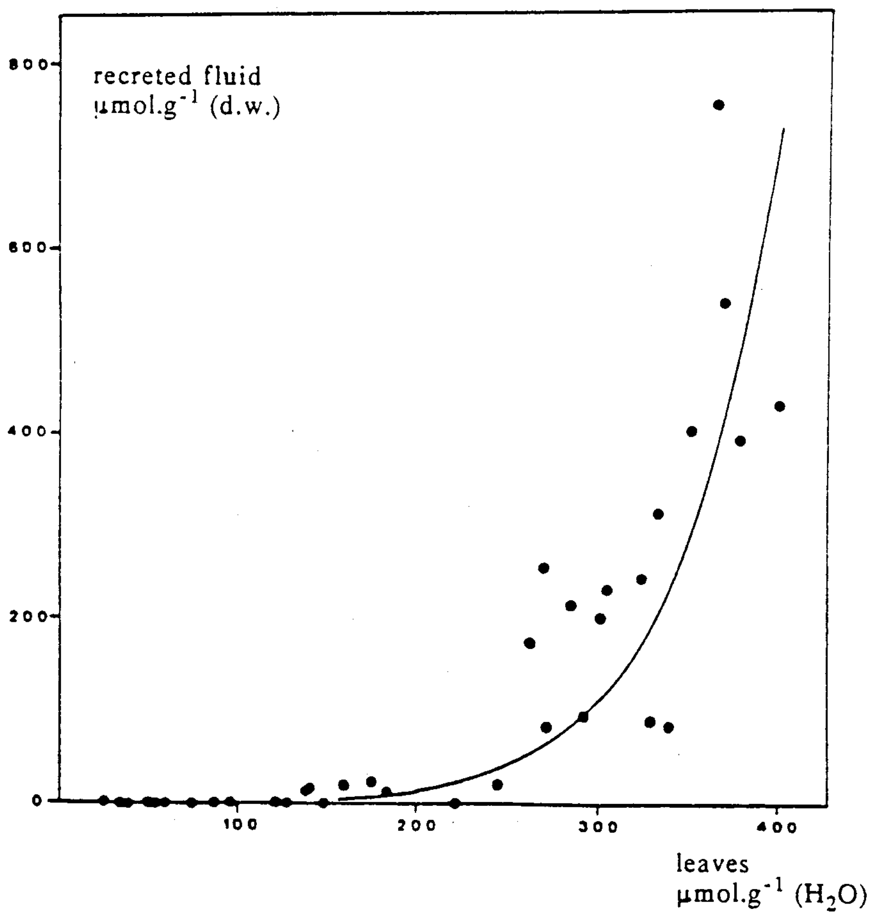

Fig. 9 : Retarded increase of chloride-concentration in recreted sap from *Limonium sinuatum* with increase of leaf-chloride-concentration in leaves (WIEHE 1986)

3.2.3 Bladders in *Atriplex*

Whereas plants with salt-glands apparently cope with salt-stress by an increased activity under higher salinities, those plants characterized by bladders have another metabolic feature. They recrete salt from the beginning, from low salt-stress on, sometimes reaching saturation already under low salt-stress (100 mM NaCl), others far beyond 250 mM. (Fig. 10).

In all *Atriplex*-species the enrichment-factor of salt in the bladder corresponding to the nutrient solution drops with increasing salinity. In Fig. 11 this is shown for *Atriplex falcata*, an dwarf-shrub of the semi-deserts in Utah, which was cultivated in sand-culture experiments with increasing salinities (BRECKLE, 1976). The same was true for *A. confertifolia*, and a similar behaviour could be shown for the annual *Atriplex hortensis* (SCHIRMER & BRECKLE 1982).

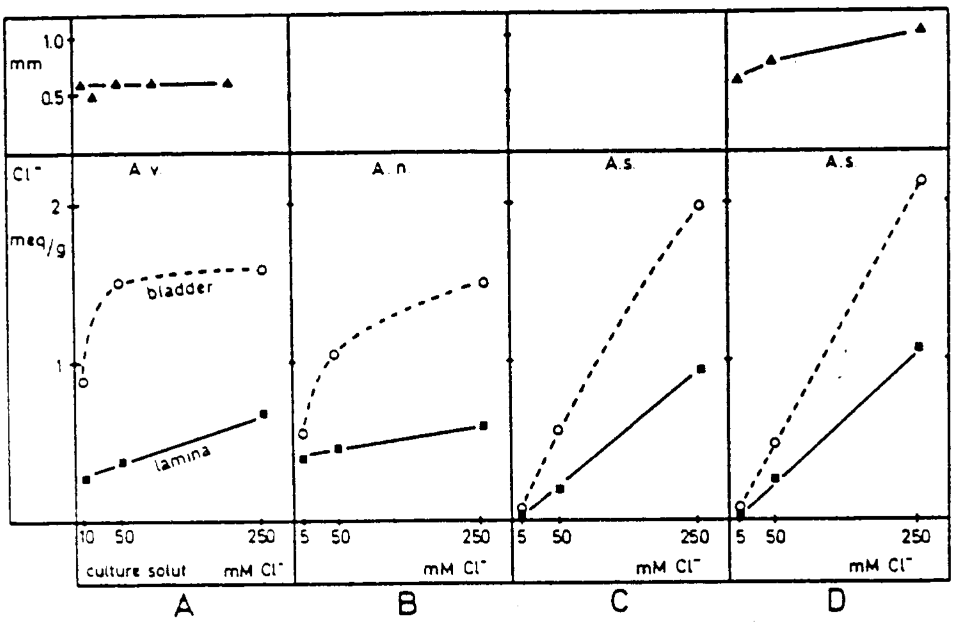

Fig. 10 : Concentrations of Cl^- in lamina and bladders of *Atriplex vesicaria* (A.v.), *A. nummularia* (A.n.) and *A. spongiosa* (A.s.) grown in nutrient solution containing NaCl. In A and D thickness of leaf lamina is indicated (OSMOND et al. 1980)

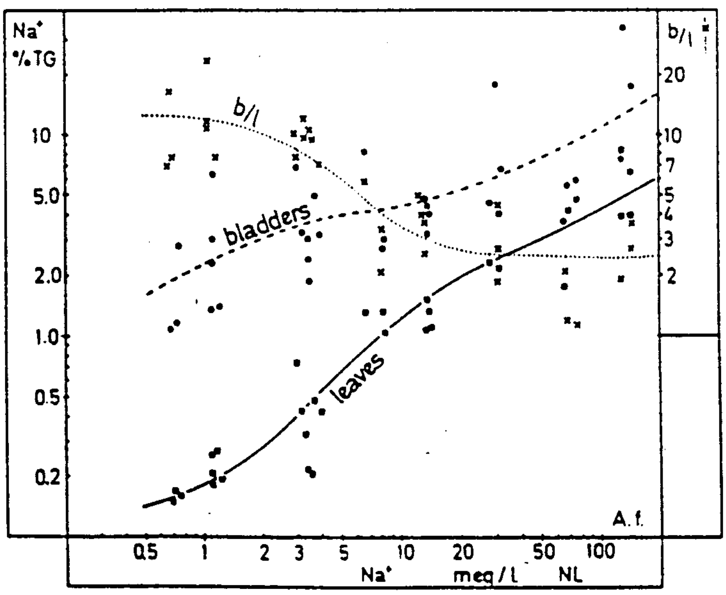

Fig. 11 : Sodium percentage in leaves (**l**) and bladders (**b**) from *Atriplex nutallii* (=*A.falcata*), cultivated in quartz sand with increasing sodium concentration in nutrient solution (BRECKLE 1976). Indicated is also the molar ratio of sodium: **b/l**

It can be shown that the accumulation ratio by bladder bearing plant species is relatively higher in *Atriplex* than in *Chenopodium*. In Tab. 4 the accumulation of Cl^--ions in bladder hair of some Chenopodiacean genera is shown.

Table 4 : Accumulation of Chloride-Ions in Bladder Hair of Atriplex-, Halimione- and Chenopodium-species (**B**: Bladder; **L**: Mesophyll)
NS: mM NaCl in nutrient-solution;
AR1: accumulation-ratio = **B/L+B**; AR2: accumulation-ratio = **B/L**

species	NS	AR1	AR2	Author
Atriplex nummularia	50	0.73	2.8	OSMOND et al. 1969
A. spongiosa	50	0,70	2.3	dto.
Halimione portulacoides	100	0.71	2.5	BAUMEIST. & KL. 1974
Atriplex confertifolia	100	0.69	2.1	BRECKLE 1976
Atriplex confertifolia	50	0.73	2.8	dto.
Atriplex falcata	100	0.59	1.4	dto.
Atriplex inflata	250	0.76	3.1	OSMOND 1979
Atriplex nummularia	50	0.71	2.5	dto.
Atriplex spongiosa	50	0.68	2.1	dto.
Atriplex vesicaria	50	0.76	3.1	dto.
Atriplex spongiosa	50	0.67	2.0	OSMOND et al. 1980
Atriplex vesicaria	50	0.71	2.5	dto.
Atriplex hortensis	100	0.70	2.4	SCHIRM./BRECK. 1982
Chenopodium album	100	0.58	1.3	REIMANN/BRECK. 1985
Chenopodium giganteum	100	0.60	1.5	dto.
Chenopodium murale	100	0.59	1.4	dto.
Atriplex littoralis	50	0.75	3.0	FREITAS/BRECK. 1992
Atriplex calotheca	50	0.84	5.3	dto.

Under moderate salinity-stress the huge amount of bladders is able to accumulate a rather high proportion of salts in the vacuoles of the bladders. Thus, these salts are removed, mainly from meristematic tissues in the plant. This seems to be the main function of bladders in those species. This is strenthened by the observation, that bladders during ontogenesis are very early formed. In very young leaves close to the vegetation tip the volume of bladders may be more than double of that of the rest of the leaf. In adult leaves the volume may be equal to that of the mesophyll.

4 General and ecological conclusions

A typical halo-series along a salt-gradient was shown by KEARNEY et al. already in 1915 from the Great Salt Lake area (Fig. 12).

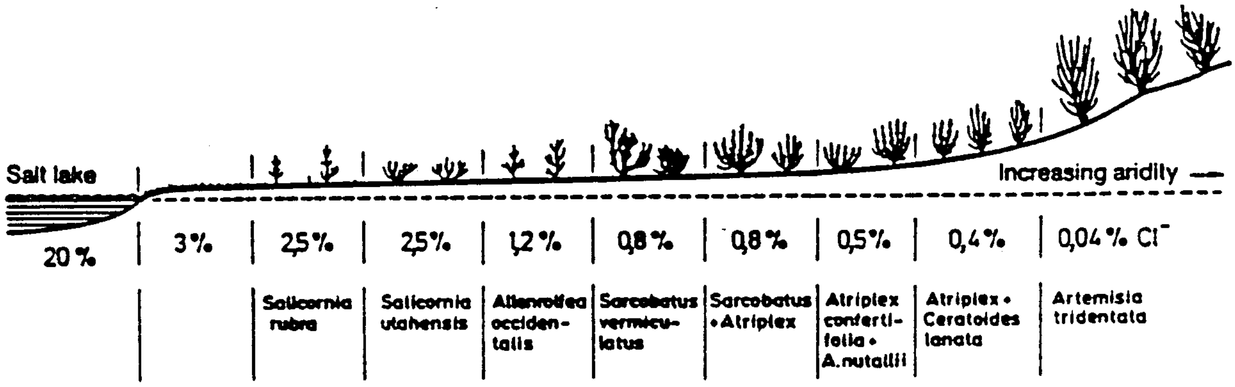

Fig. 12 : Diagrammatic profile of the haloseries on the shore of the Great Salt Lake, Utah (USA) showing chloride percentage of dry soil weight in the individual vegetational belts (KEARNEY et al. 1914, BRECKLE 1976)

Under natural conditions with high competition it was shown by BRECKLE (1986, 1989, 1990), that the halo-series in those floristic areas, where enough halophytic species and types are present (this is dependent on vegetation history), a distinct sequence of life-forms and halophyte-types develops. This can be taken as proof for the competitive force of the halophyte-types. Almost in all investigated salt-deserts (Namib, Australia, Atacama, Afghanistan, Iran, Uzbekistan, Negev, Sahara, Utah) or along salty lakes (Spain, Romania, Turkey, Israel, South Africa) the sequence of halophyte-types was more or less similar. At the most saline end (which is also more moist) stem-succulent Eu-Halophytes dominate and are within the halo-series intermixed with leaf-succulent ones, which often have a rather wide range. On moderate salinities (often more dry) mainly the various types of recreting halophytes occur and have to cope with a wide amplitude of salt-stress and partly as well as with drought-stress. To the less saline side in the sequence other pseudo-halophytes and non-halophytes intergrade and lead to the zonal vegetation mosaic.

Summarizing conclusions:

- salt-glands have evolved several times independantly in higher plants and are found in several different plant families -- forced by salt-stress
- bladder structures with glandlike stalk cells are typical for some genera in Chenopodiaceae
- activity and selectivity for ions differs from genus (species) to genus (species)
- Along salt gradients (natural stands, salt lakes) recreting halophytes have their ecological optimum (with few exceptions) mostly on moderate salinities (paralleled by moderate aridity?)
- Thus recretion of salts is only one of several adaptations to cope with salt-stress, but a very interesting one: with a very close correlation of structure and function!

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