

# THE SALT GLANDS OF *SAMOLUS REPENS*

PAUL ADAM AND BARBARA M. WIECEK

School of Botany  
University of New South Wales  
Kensington NSW 2033

## INTRODUCTION

For saltmarsh and mangrove plants it would seem that "Life wasn't meant to be easy". In addition to the problems that all plants face in growing in natural multispecies communities coastal halophytes are presented with especial challenges inherent in inter-tidal environments. These include:

- high, and variable, soil water salinity;
- soil conditions which may be anaerobic for long periods;
- mechanical problems associated with tidal movement.

These may be particularly important in seedling establishment and the tidal scouring of newly germinated seedlings is probably a major factor preventing the seaward spread of a number of species.

The majority of research on adaptation of halophytes to their environment has been with respect to salinity problems while other aspects of the saltmarsh environment, especially the anaerobic soil conditions, have been comparatively neglected.

The presence of high salt concentrations in the root environment might be expected to influence both the ionic and water balance of plants. The ionic constitution of the soil solution is likely to be very different from that required for optimal plant nutrition; halophytes are thus faced with the problem of obtaining sufficient nutrient ions from a solution dominated by ions which are not required in large amounts for plant nutrition and which might even become toxic if present in the cytoplasm in large amounts. In addition the presence of salt in the soil solution will cause a lowering of the soil water potential (that is to say the soil solution will have a high osmotic pressure). If plants are to be able to absorb water from such a solution then the water potential of the plant tissue must be lower still.

Measurements of plant tissue water potentials suggest that, while halophytes may undergo brief periods of severe water deficit, in general water potentials in saltmarsh plants are lower than those in the soil solution. How are the low water potentials achieved? In view of the ready availability of ions in the external environment one way would be to challenge fire with fire and absorb ions until the internal concentration of salt is greater than that externally. Most saltmarsh plants do contain large quantities of salt and indeed in the past various saltmarsh plants have been harvested and burnt to yield an ash for use in glass or soap manufacture.

Recent research suggests that while salt absorption is a major factor in the generation of low tissue water potential the story is more complicated. One problem is that we cannot yet be completely certain as to where within the tissues these large amounts of salt are accumulated. Studies on the effect of salt on enzyme activities indicated that the enzymes of halophytes are not significantly different from those of other plants and that the metabolism of halophytes would function if the enzymes were in contact with the salt levels implied by the gross tissue salt content. From findings as these there has developed the view that there must be considerable differences in salt concentration between compartments within the cell. It is generally assumed that the majority of the salt must be sequestered in the vacuole and cytoplasmic concentrations must be low in order to protect enzyme function. However, the water potential of cytoplasm and vacuole must be the same so that there must be other solutes, compatible with enzyme function, in the cytoplasm in order that conditions for uniform water potential are satisfied. A number of organic compounds have now been detected in different halophytes which would seem to have the properties of cytoplasmic osmoregulators. These substances have little effect on enzyme activity, even at high concentrations, and their abundance in plant tissues varies with external salinity conditions. Compounds with these properties in various halophytes include the imino acid proline, quaternary ammonium compounds (especially glycine betaine) and the sugar alcohol sorbitol. It is interesting that many of the suggested osmoregulators are nitrogen containing compounds; this may explain the fact that nitrogen has often been shown to be a limiting factor to the growth of saltmarsh vegetation and that saltmarsh plants respond vigorously to nitrogenous fertilisers.

Nevertheless, while ion uptake has an important part to play in the generation of low water potentials, the process must clearly be controlled lest, like Lot's wife, halophytes end up as pillars of salt. There are four basic strategies, which, either separately or in combination, halophytes have adopted to regulate the ionic concentration of their tissues.

#### 1) Limitation of uptake.

In all halophytes that have been investigated the ionic concentration of the xylem sap is lower than that of the soil solution at high salinities implying some control of ion uptake presumably in the root. Little is known about root function of halophytes and whether the control processes are active or passive remains open to doubt. The degree of ion exclusion appears to vary between species and is greatest in those plants which do not possess other well developed mechanisms for ion regulation. This is clearly seen in a comparison of the ion-excreting mangrove *Aegialitis annulata* with the non-excreting *Rhizophora mucronata* (Atkinson *et al.*, 1967), in both species xylem sap was far less concentrated than sea water, but while *Aegialitis* sap had a chloride concentration of 85-122 mol. m<sup>-3</sup>, that of *Rhizophora* was only 17 mol. m<sup>-3</sup>.

Nevertheless, even if the salt concentration of the xylem sap is low, salt is constantly being carried up into the leaves and shoots. In young tissue the build up of salt concentration can be minimised by growth (i.e. while tissue is expanding the potential storage volume for salt is increasing so that if the growth rate is appropriate for the xylem sap salt concentration then the tissue salt concentration can be maintained approximately constant). However, once growth ceases, (and all leaves have a finite size), then it is inevitable that salt will build up in the tissue. When leaves are shed by even the most effective root excluder they invariably contain a relatively large amount of salt.

#### 2) Development of succulence.

Many coastal plants are succulent with leaves and young stems that feel soft and fleshy to the touch. They contain large numbers of relatively thin walled cells with very large vacuoles.

Succulence can be viewed as a means of maintaining internal salt concentration at an appropriate level through dilution. If much of the salt taken up by the plant is stored in cell vacuoles then the concentration of the internal salt solution will be determined by the vacuolar volume. This concentration has to be sufficient to at least balance that in the soil solution but as more salt continues to be carried to the leaves in the transpiration stream, the concentration would increase unless it were maintained constant by continual dilution. Dilution would require further uptake of water and this is accommodated for by an increase in the size of the vacuole. Many plants on sand dunes and sea cliffs, which are exposed to moderate salt stress, respond by becoming more succulent than members of the same species from inland habitats. On local saltmarshes species such as *Sarcocornia quinqueflora* and *Suaeda australis* are notably succulent.

Many plants of arid regions are also succulent and in this case succulence is either a direct water storage mechanism or is concomitant on the possession of a modified pathway of photosynthesis - (crassulacean acid metabolism CAM - see Kluge and Ting 1979). For saltmarsh plants water is generally readily available, even if its chemical potential is low, and there are no known examples of an inter-tidal halophyte employing the classic CAM pathway.

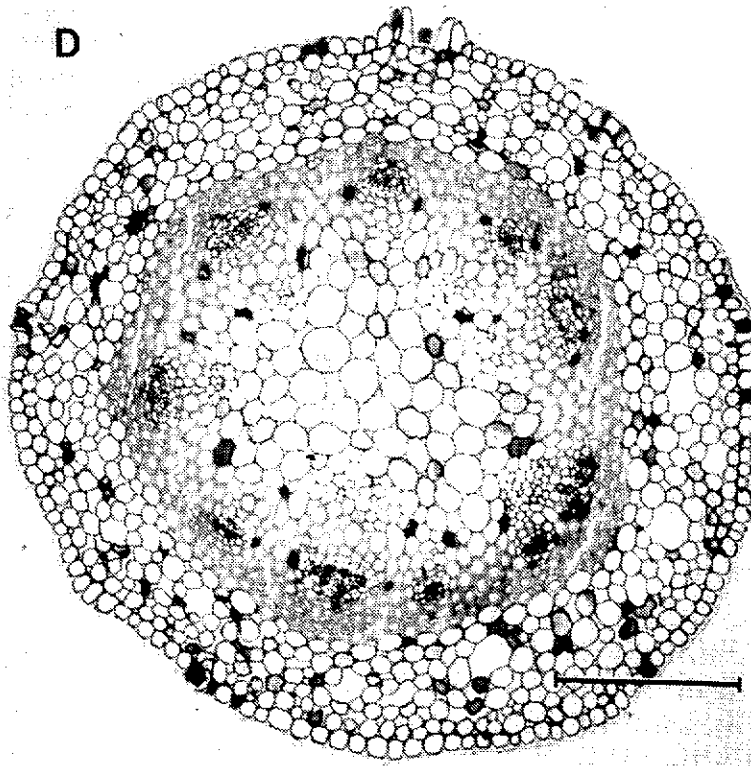
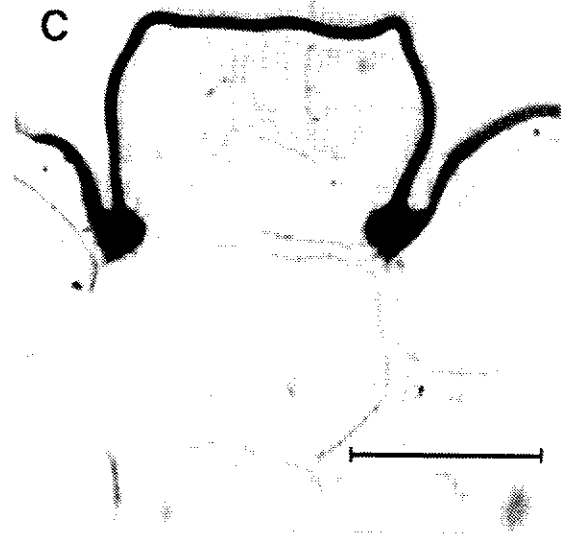
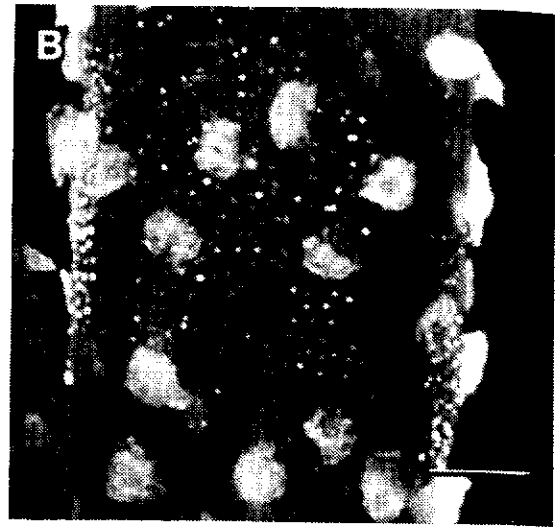
#### 3) Secretion of excess salt through specialised structures known as salt glands.

#### 4) Shedding of salt laden parts.

The various salt regulatory mechanisms serve to delay but not prevent the inevitable and tissue salt concentrations are likely to reach lethal levels eventually. In some widespread saltmarsh species, notably the rushes (*Juncus* spp.), there is little development of succulence and no salt glands. The extent of salt exclusion in the roots has not been investigated for most of these species but from our knowledge of halophytes generally it would be reasonable to assume a considerable degree of exclusion. Once the leaves and stems have ceased growth tissue salt content increases but there is a rapid turnover of organs so that as salt builds up, organs are shed and replaced by new growth. Before the old parts are shed, some minerals of use to the plant are translocated into the new growth and the shed organs contain a predominance of sodium chloride.

### SALT GLANDS OF AUSTRALIAN COASTAL HALOPHYTES

Salt glands are possessed by relatively few species of halophytes. Nevertheless, a great deal of attention has been paid to them by both anatomists and physiologists, although even today nearly a hundred years after the first investigations on salt glands, we are still far from understanding how salt glands in any species function. Earlier studies on salt glands include Volkens (1884), Klugh (1909), Haberlandt (1914) and Ruhland (1915), while recent reviews of salt gland structure and function include Thomson (1975), Lüttge (1975), Hill and Hill (1976) and Fahn (1979).



Salt glands have been reported from a wide range of species (Waisel 1972; Lüttge 1975; Hill and Hill 1976). There are no obvious relationships between all the taxa with salt glands and it seems probable that salt glands have a polyphyletic origin. There is considerable diversity in gland structure and it seems likely that glands evolved either from existing glandular structures or non-glandular trichomes within each major taxonomic group in which salt glands are found.

A number of Australian mangrove species have been shown to possess salt glands; *Avicennia*, *Aegiceras*, *Aegialitis*, *Acanthus* and possibly *Sonneratia* (Clough and Andrews 1981). Both mangroves found near Sydney, *Aegiceras corniculatum* and *Avicennia marina*, have well developed salt glands which are easily observed (see illustrations in Curran and Goulter 1982). The salt glands of *Aegialitis annulata* have been investigated physiologically by Atkinson *et al.* (1967) while those of *Aegiceras corniculatum* have been subject to both anatomical and physiological studies by Field (Cardale and Field 1971; Bostrom and Field 1973 and Billard and Field 1974).

Australian saltmarsh plants do not seem to have been surveyed for the occurrence of salt glands. On the basis of the observation of salt crystals on leaf surfaces and the presence of structures similar to those described as salt glands from related species overseas, we can report the probable possession of salt glands by a small number of Australian species.

The salt glands of grasses are relatively small, two-celled structures (Waisel 1972; Thomson 1975; Hill and Hill 1976) which can be difficult to distinguish from various other epidermal protruberances in hand-cut leaf sections. Nevertheless, when combined with observations of salt crystals on the leaves, we suggest that the widespread saltmarsh grass *Sporobolus virginicus* possesses salt glands (see also Smith-White 1977). *Distichlis distichophylla*, which is the ecological equivalent of *Sporobolus* on marshes in Tasmania and parts of Victoria and South Australia, also has glands similar to those described from the American *D. spicata* (Anderson 1974). We have also observed glands in the introduced *Spartina anglica*.

The salt glands of dicot species are also much larger than those of the grasses and can be easily detected on leaf sections.

The salt glands of the sea lavenders (*Limonium* spp.) have been the subject of more study than those of any other genus. We have observed salt glands in the native *L. australe* and also in two introduced species, *L. binervosum* and *L. psilocladon*.

The dwarf shrub *Frankenia pauciflora*, which is widespread in the upper saltmarshes along the south coast of Australia, has well developed complex glands similar to those described from the Californian *Frankenia grandifolia* by Campbell and Thomson (1976).

#### THE SALT GLANDS OF *SAMOLUS REPENS*

During the course of field work on local saltmarshes, we observed that during the summer, the leaves of *Samolus repens* (Forst. *et* Forst. f) Pers. were often dotted with salt crystals. This strongly suggested the presence of salt glands and simple hand-cut sections of leaves revealed the existence of structures similar to those described as salt glands from other dicots.

Closer examination of leaves has shown that the salt crystals on the leaf surface are restricted in their occurrence to immediately above the glandular structures, while analysis of solutions obtained by washing leaves with distilled water showed sodium to be the major cation. There are thus strong grounds for believing that *Samolus repens* has salt glands although physiological experiments are required to prove this conclusively.

*Samolus repens* is one of the most widespread herbs on New South Wales saltmarshes. Although rarely dominant, except in small patches, it is found scattered in most marsh communities. In addition, it is characteristic of wet ledges and crevices or seacliffs. *S. repens* is variable in appearance (Adam 1981) but it is a plant which spreads extensively through the production of runners from an original rosette. Daughter rosettes are formed on the runners and readily take root. Flowering is often prolific, the individual flowers are small, up to a maximum of 1cm in diameter, and white to pale pink in colour.

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Photo 1 - A & B, salt crystals on leaves of *S. repens* - scale bar A = 5mm, B = 1 mm: C, gland on leaf, cuticle stained with Sudan Black B in 70% ethanol - scale bar = 20  $\mu$ m: D, cross section of stem, stained with Toluidine Blue, note gland with adjacent protuberant epidermal cells - scale bar = 200  $\mu$ m: E, gland on stem, cuticle stained with Sudan Black B in 70% ethanol - scale bar = 25  $\mu$ m.

*Samolus* is a member of the family Primulaceae. The family is not generally regarded as being a major constituent of saltmarsh vegetation but in the northern hemisphere *Glaux maritima* is a very widespread saltmarsh species. Studies by Rozema, Riphagen and Sminia (1977) and Rozema and Riphagen (1977) have demonstrated the occurrence of salt glands in *Glaux*. We are not aware of any previous reports of the existence of salt glands in any species of *Samolus*. However, a wide variety of secretory structures has been recorded from terrestrial members of the Primulaceae (Metcalfe and Chalk 1950). Secretory cavities, containing a red crystalline material are reported from the leaves of a number of Primulaceae including species of *Samolus* and what are referred to as secretory cells have been observed in the stems of *Samolus valerandi* (Metcalfe and Chalk 1950).

#### DISTRIBUTION OF GLANDS

Hand-cut sections of leaf material from a number of New South Wales *S. repens* populations all revealed the presence of glandular structures.

It was decided to investigate the distribution of glands in more detail and to see whether the gland frequency changed depending on whether the plants were growing in fresh or saline solutions.

A plant of *S. repens* collected from a saltmarsh at Budgewoi on Tuggerah Lake on 20 February 1980 (Voucher number UNSW 14118) was vegetatively replicated in the greenhouse by separating daughter rosettes produced on runners. During this period the plants were grown in a mixture of loam and sand and watered with tap water.

On 27 July 1981 ten daughter plants were allocated at random to each of two treatments, freshwater and saltwater. The plants were placed in pots which were suspended above large, polythene lined tanks which contained either tapwater or 10% seawater. The pots were arranged such that the water table in the soil was about 2cm below the soil surface. The solutions in the tanks were changed at fortnightly intervals and at the same time the positions of the pots within each treatment were changed. At six weekly intervals all pots in both treatments were top watered with one tenth strength Hoaglands nutrient solution.

The salinity of the saltwater treatment was much lower than the maximum salinity likely to be attained in the field. There were no obvious differences in vigour between the two treatments, but pots in the seawater treatment did not require weeding as frequently as those in freshwater.

At the start of the experiment, ten leaves were sampled at random from each of the treatments. The whole leaves were cleared and examined using the 40x objective of a Zeiss Standard RA microscope. For each leaf, the number of glands per field of view was counted for ten randomly chosen fields from both upper and lower leaf surface. The procedure was repeated on a further seven occasions at approximately six weekly intervals with the last collection on 5 February 1982. As far as possible, ten fields of view were counted per leaf surface but in some cases with very small leaves this was not possible and a lesser number of fields had to be used.

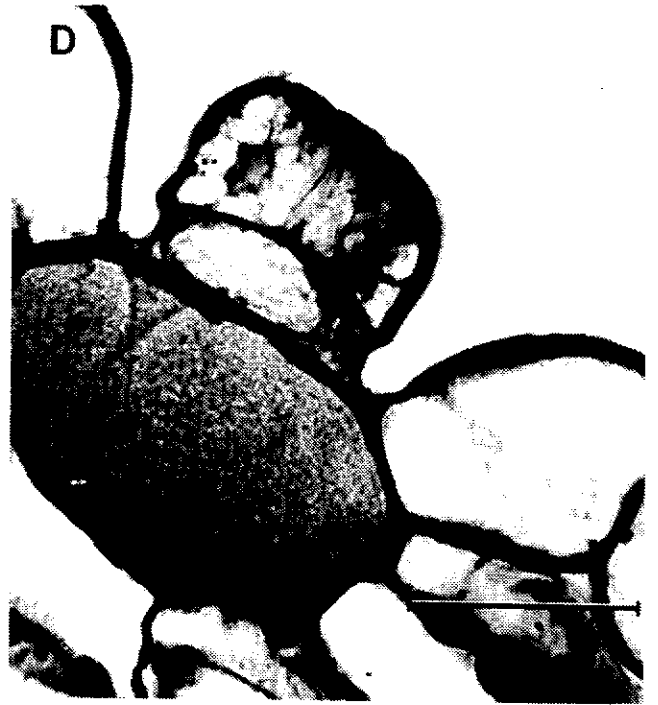
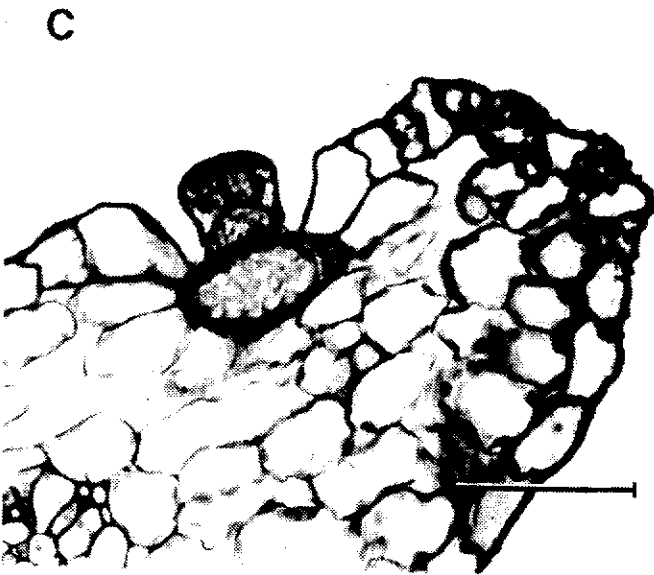
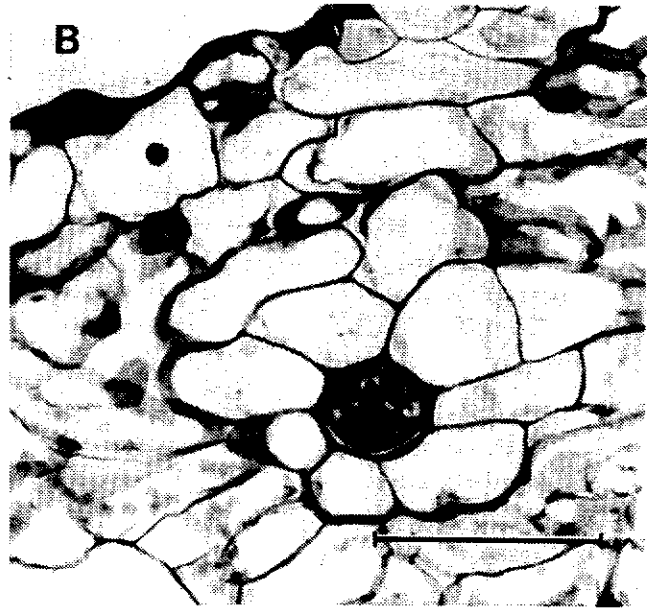
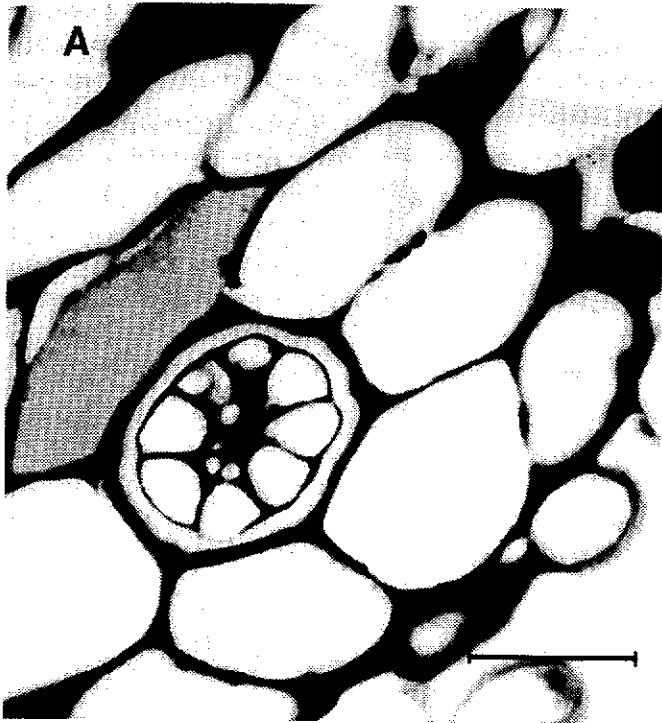
The number of glands observed was very variable. However, there was no consistent variation in gland density with position on the leaf nor was there any significant difference between the two epidermides. There was no significant difference between the gland densities in the two treatments and the number of glands in the saltwater treatment did not increase during the course of the experiment.

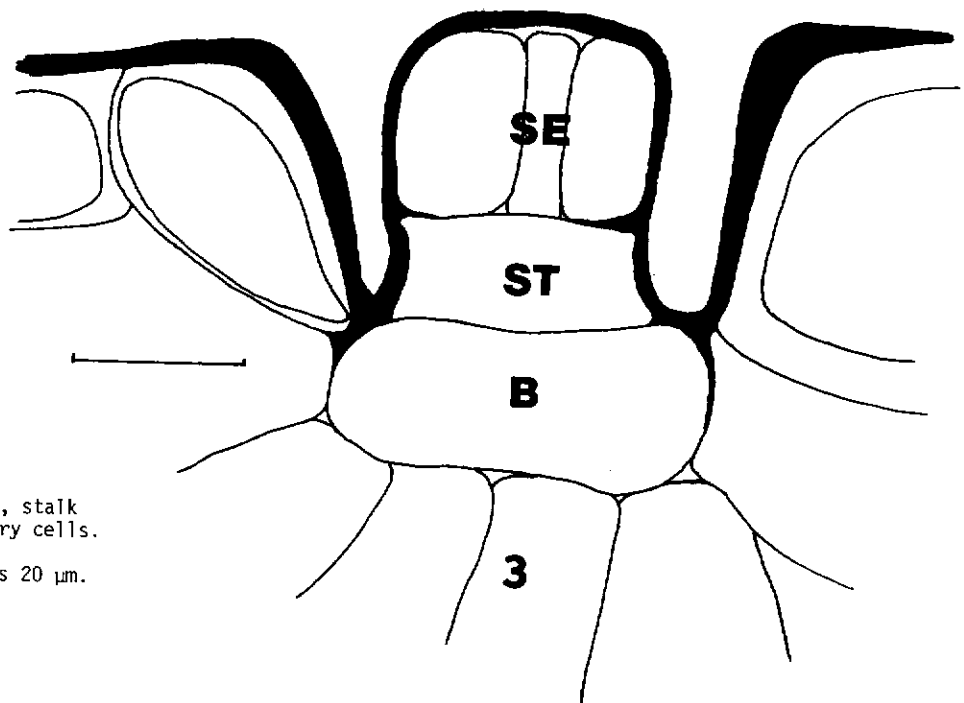
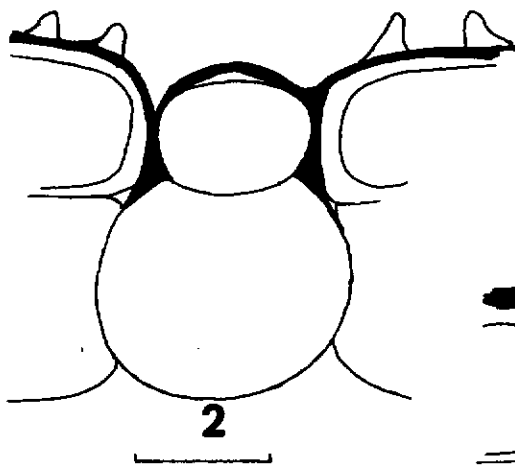
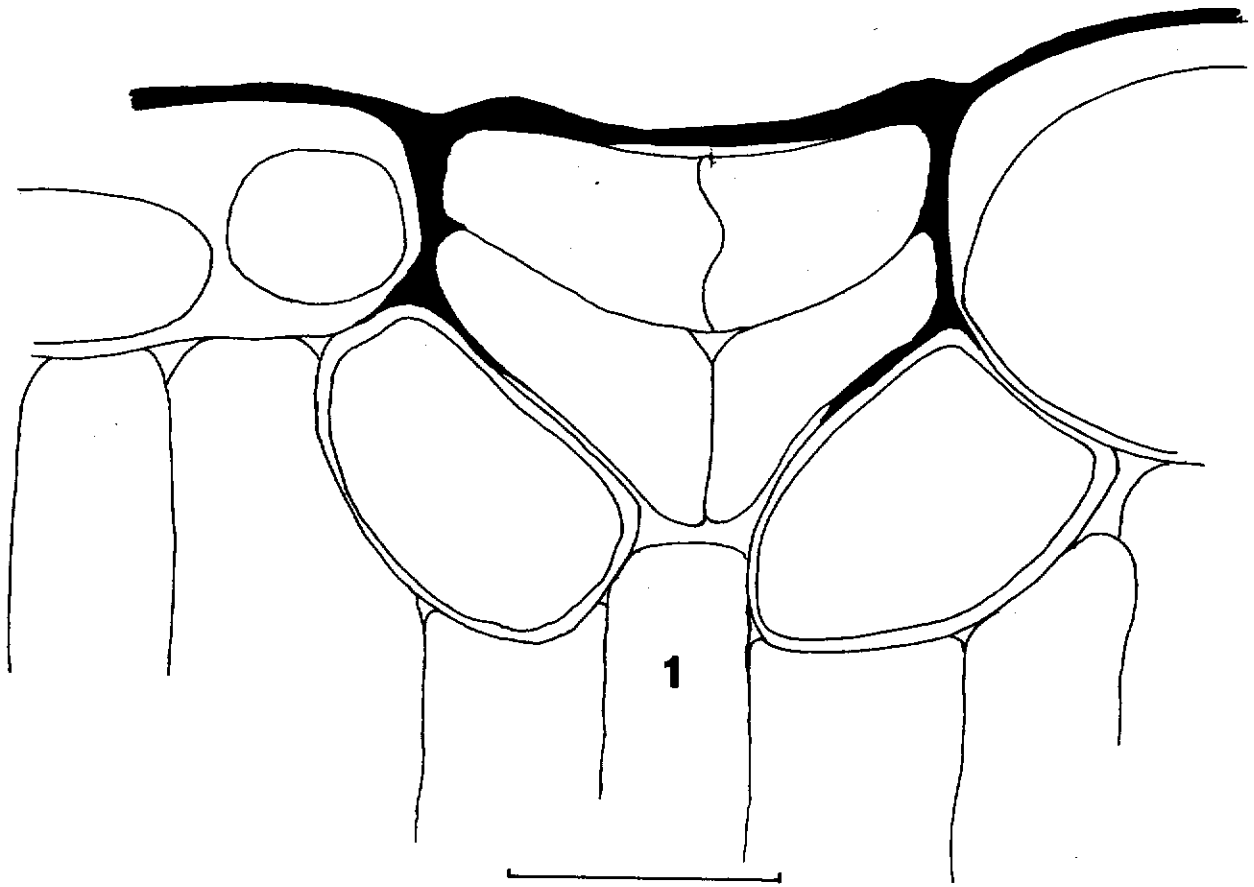
Overall the mean gland density was  $1103 \pm Sd518 \text{ cm}^{-2}$  of surface (based on 160 leaves). This figure is more than twice that reported for *Glaux maritima* by Rozema *et al.* 1977, but is low compared with some of the densities reported from other halophytes by Waisel (1972). Given the wide variation in form of *S. repens* and the range of habitats it occurs in, it is possible that gland density may vary between populations but this has not been investigated.

In addition to occurring on the leaves, glands are also found on the stems. This is in contrast to *Glaux* in which Rozema *et al.* (1977) report the absence of glands on the stems.

Examination of cotyledons of newly germinated *S. repens* has shown that glandular structures are present at this stage also.

Photo 2 - A & B, near paradermal sections through glands showing variation in the arrangement of cells within the gland complex. Sections stained with Periodic Acid Schiff's reagent and Toluidine Blue - scale bar A = 25  $\mu\text{m}$ , B = 80  $\mu\text{m}$ ; C, gland on upper surface of leaf, stained with Toluidine Blue, there is a little differentiation of spongy and palisade mesophyll in *S. repens* - scale bar = 50  $\mu\text{m}$ ; D, gland on upper surface of leaf, stained with Toluidine Blue - scale bar = 20  $\mu\text{m}$ .





SALT GLANDS OF VARIOUS SPECIES

1. *Frankenia pauciflora*
2. *Spartina anglica*
3. *Samolus repens* - B, basal cell, ST, stalk cell, SE, secretory cells.

The scale bar on each drawing represents 20  $\mu$ m.  
The cuticle is shown in heavy black

## ANATOMY OF THE SALT GLANDS

Small pieces of leaf and stem tissue were prepared for microscopy. After fixation and dehydration the specimens were embedded in glycol methacrylate (GMA)/Quetol (Kushida, Negato and Kushida 1975), which was subsequently polymerised by heat treatment at 60°C. The blocks were then sectioned using a glass knife to produce sections 1 µm in thickness. Sections were mounted on slides and stained by various procedures prior to examination.

The salt glands are sunk in pits in the epidermis. The epidermal cells surrounding the pit have a very thick cuticle which forms a distinct ridge around the pit. The glands are very similar in appearance to those described from *Glaux* (Rozema *et al.* 1977) and, using the same terminology, a basal (or collecting) cell, a stalk cell and a group of secretory cells can be recognised. The gland is invested with a well developed cuticle. The secretory cells contain dense granular cytoplasm, relatively large nuclei and numerous small vesicles but no large vacuoles. The other cells of the gland are similar in content. Rozema *et al.* (1977) describe the basal cell of *Glaux* as containing a large central vacuole and rather poorly developed chloroplasts. In *Samolus* chloroplasts have not been observed in any cells of the gland but in a number of instances a relatively large vacuole was seen in the basal cell.

In near paradermal sections the thick cuticular ridge of the epidermal cells surrounding the gland pit can be seen clearly. The epidermal cells surrounding the pit are more nearly isodiametric than those in the epidermis in general but the number of cells around each pit is variable, unlike *Glaux* where Rozema *et al.* (1977) report the regular occurrence of six cells. In the majority of sections examined the secretory cell complex contained six to eight unequally sized cells, but in other sections up to twelve cells formed the secretory complex. In some salt glands (for example, *Limonium* Hill and Hill 1976) there is clear evidence for the existence of pores in the cuticle over the gland through which a salt solution is exuded. In others, for example, *Aegioeras* (Cardale and Field 1970) and *Glaux* (Rozema *et al.* 1977) there are no obvious pores and the means by which salt is excreted through the cuticle remains unknown. There is no indication in our sections of any pores in the cuticle over the glands in *Samolus repens* but this requires confirmation from scanning electron microscope studies. In some species a distinct gap has been recorded between the gland cells and the overlying cuticle. A similar feature has been observed in the secretory trichomes of the *Abutilon* nectary (Gunning and Hughes 1976). A similar gap occurs between the secretory cells and the cuticle in some of our sections.

The salt glands in the stems are similar in structure to those in the leaves but are sunken in deeper pits, which are produced as a result of the surrounding epidermal cells protruding considerably above the general level of the epidermis. The glands in the cotyledons generally appear similar to those in the leaves. However, in some instances the stalk cell is attached, not to a single large basal cell, but to at least two relatively small cells.

The glands in *Samolus* are similar in many respects to those described from other dicots. General features of salt glands are the lack of any obvious connection between glands and the vascular system and the absence of chloroplasts from the majority of cells in the gland complex. The pathway for salt entry into glands and the source of the energy requirements for active secretion thus being topics for speculation.

A feature of several salt glands which have been investigated is the occurrence, particularly in the so-called secretory cells of numerous protruberances of the cell wall which support infoldings of the plasma membrane. Such cells are referred to as transfer cells (Pate and Gunning 1972). At the light microscope level of investigation, these are not visible in *S. repens* (unlike *Frankenia pauciflora* where they may be clearly seen), but electron microscopy is required to check for the presence of this feature.

During the course of the experiment to investigate the possibility of changes in gland frequency described above, material from each treatment was fixed at various times and sections cut. At the light microscope level of investigation there were no differences apparent between the fresh and saltwater treatments. It would be of interest to carry out electron microscopy in order to see whether there are differences in ultrastructure between the treatments.

## OTHER SPECIES OF *SAMOLUS*

The genus *Samolus* is a small one of only 10-15 species (Airy-Shaw 1966). The genus is cosmopolitan in distribution but with more species in the southern hemisphere. The majority of species occur in wetland habitats and some species are common in brackish or saline marshes.

Four species are currently recognised in Australia: *S. repens*, *S. junceus* R. Br., *S. eremaeus* Jacobs and *S. valerandi* L. *S. junceus* is a Western Australian species which differs from *S. repens* in having relatively few basal leaves and totally leafless stems. 'Good' examples of *S. junceus* are very distinctive. However, there are plants in Western Australia which are midway in appearance between *S. repens* and *S. junceus*. It is possible that these forms represent an, as yet, undescribed taxon or they may indicate that 'good' *S. repens* and *S. junceus* are but the end points of a continuum of variation and that recognition of two species may be unnecessary. Further taxonomic work is required on this complex.



*S. eremaeus* is a recently described species (Jacobs 1980) from inland Central Australia, which, in overall appearance is similar to *S. valerandii*. *S. valerandii* is a widespread species in Europe which also occurs widely in coastal Australia. Some flora writers have suggested that it was introduced to Australia but the general consensus seems to be in favour of it being a native species.

We have examined herbarium specimens of the various *Samolus* species. After rehydrating fragments of leaf tissue, it is possible to observe glandular structures if they are present. Glands have now been recorded from *S. junceus* and from various specimens intermediate between *S. repens* and *S. junceus*. *S. eremaeus* possesses numerous glands similar in appearance to those of *S. repens* and *S. junceus*.

Various aspects of the biology of European populations of *S. valerandii* have been studied by one of us (P. Adam). In the course of these studies there was no indication that the species possessed salt glands. We have examined a small number of specimens of *S. valerandii* from eastern Australia. In these we did not observe any glands with the structure described above from other *Samolus* species. However, the leaves did contain numerous single, and small groups of, cells with amorphous orange contents which possibly correspond to the secretory cells reported by Metcalfe and Chalk (1950). It would be appropriate to carry out a broader survey of *S. valerandii* populations but our preliminary results may indicate that, despite initial superficial appearances, *S. eremaeus* has closer affinities to the *S. repens* group than to *S. valerandii*.

## DISCUSSION

Our investigations are of a preliminary nature only and there remains to be done much anatomical work at the electron microscope level to investigate the ultrastructure of the glands. It would also be valuable to carry out physiological studies in order to assess the contribution of the salt glands to the achievement of an overall salt balance by *S. repens*.

It would be of interest to grow *S. repens* at higher salinities than we have used. With *Glaux* Rozema *et al.* (1977) suggest that there was slight increase in gland frequency at higher salinities (i.e., up to 300mM - which is in excess of 50% sea water). As such salinities may be exceeded for long periods in saltmarsh soils supporting *S. repens*, it is realistic to challenge experimental plants with much higher salinities than we used. It would also be of interest to investigate whether the glands of plants grown in fresh water are instantly functional if the plants are transferred to high salt conditions or whether a period of acclimation is required.

As we stressed earlier in this paper very few saltmarsh plants in Australia have been examined to see whether they possess salt glands. Our initial observations were made on simple hand sections. It would be an easy exercise to survey the saltmarsh flora for the possible occurrence of salt glands, any species showing the possible presence of glands in hand sections could be subject to more detailed investigations subsequently. We would be very interested to hear of other species which may have salt glands.

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