SALT REGULATION IN THE MANGROVES *RHIZOPHORA MUCRONATA* LAM. AND *AEGIALITIS ANNULATA* R.BR.

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Summary

The mangrove *Rhizophora mucronata* grows in an intertidal region and excludes salt from its xylem (17 m-equiv. chloride per litre of sap) more efficiently than does the salt-secreting mangrove *Aegialitis annulata* (85–122 m-equiv. chloride per litre of sap). From the transpiration stream each leaf of *Rhizophora* receives about 17 μ-equiv. chloride each day, but the chloride concentration of the growing leaf remains approximately constant (510–560 m-equiv. chloride per litre of sap water). In *Aegialitis* input of chloride to a mature leaf is about 100 μ-equiv. per day and this input is balanced by secretion (mainly of sodium chloride) from the salt glands. Secretion collected under oil contains chloride, 450 μ-equiv/ml, sodium, 355 μ-equiv/ml, and potassium, 27 μ-equiv/ml. Secretion rates from leaves on the tree, based on leaf area, vary from 93 p-equiv. cm^{-2} sec^{-1} during the day to 3 p-equiv. cm^{-2} sec^{-1} in darkness; the secretion in light, based on an effective gland area, is about 25,000 p-equiv. cm^{-2} sec^{-1}. The water potential of the secretion is close to that in the leaf suggesting that secretion involves active transport of salt and passive movement of water by local osmosis.

Salt secretion is inhibited by carbonyl cyanide 3-chlorophenylhydrazone applied to the cut petiole or to the leaf surface. Cut leaves secrete salt in darkness at approximately the same rate as in light, in contrast to leaves on the tree.

With infused radioactive chloride, the specific activity of chloride in the secretion reached a higher value than the mean value in the leaf, suggesting that some chloride passes freely from the leaf veins to the salt glands without equilibrating with the main chloride pool of the leaf.

Light- and electron-microscope studies of the glands of *Aegialitis* are described.

I. Introduction

In earlier work on the physiology of mangroves, differences between mangroves that regulate salt content mainly by excluding it from the roots, and those that also secrete salt from the leaves have been discussed (Scholander *et al.* 1962).

In this paper a comparison is made of *Rhizophora mucronata* Lam., which partially excludes salt from the xylem, and *Aegialitis annulata* R.Br., which secretes salt from glands in the leaves. These leaves are normally covered with crystals of salt left after evaporation of the secreted solution. Aspects of secretion of salt by leaves of *Aegialitis* have been studied both with leaves on the tree and with cut leaves in the laboratory. This paper also reports a study of the structure of salt glands of *Aegialitis* by light and electron microscopy.

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II. Materials and Methods

Rhizophora and *Aegialitis* trees growing in the intertidal zone on Flinders Island, in Princess Charlotte Bay, N. Qld., were studied. Transpiration was measured by placing thermocouples in the xylem equidistant from a region that was kept at an elevated temperature (approx. 10 degC above ambient), and observing the temperature distribution in the steady state (Saddler 1965). The system was subsequently calibrated against a potometer, using the same stem cut from the tree.

Chloride was measured by titration with $Hg(NO_3)_2$ using diphenylcarbazone as the indicator (Scholander *et al.* 1962), or by potentiometric titration. Sodium and potassium were measured by flame photometry, calcium and magnesium with an atomic absorption spectrometer.

Table 1

SALT CONTENT OF *RHIZOPHORA* LEAVES

Values are means for five leaf pairs; sample 1 was the youngest leaf in a sequence of increasing age

	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5	Sample 6
Dry weight (g)	0·16	0·50	0·50	0·61	0·57	0·63
Water (% of fresh wt.)	56	65	66	65	67	69
Na^+ (μ-equiv/leaf)*	61(305)	290(313)	420(431)	480(435)	520(461)	645(461)
K^+ (μ-equiv/leaf)*	24·8(124)	81(88)	57(58·5)	48(43·5)	69(61)	45(32)
Cl^- (μ-equiv/leaf)*	74(370)	520(562)	510(522)	585(530)	580(515)	730(522)

* Mean concentrations (μ-equiv/ml of leaf water) in parentheses—for details see Section III.

Balancing pressure referred to below is that pressure, applied to a leaf or leaves in an aluminium "bomb" (Scholander *et al.* 1966), which just causes xylem sap to appear at the end of the stem exposed to atmospheric pressure.

In electron-microscope studies, actively secreting leaves from *Aegialitis* trees were sliced into 1 mm squares and fixed in $KMnO_4$ buffered with veronal acetate (Luft 1956) for 3 hr. The material was dehydrated in a graded ethanol series (25, 50, 75, and 100%, with three changes in the absolute ethanol), embedded in Araldite, and sectioned on a Si-Ro-Flex ultramicrotome. After staining with lead citrate (Reynolds 1960) sections were examined in a Siemens Elmiskop 1A electron miscroscope.

III. Results

(*a*) *Salt Regulation in* Rhizophora

Over 3 successive days a shoot of *Rhizophora* with 10 leaves transpired an average of 10·3 g per day. After removal of the shoot from the tree its sap was found to contain 17 mN chloride. The shoot thus took up about 170 μ-equiv. of chloride each day or about 17 μ-equiv. per leaf per day.

Table 1 gives some measurements made on successive leaf pairs of such a shoot. Sample 1 was the unopened leaves at the tip, and sample 6 the yellowish green basal pair of leaves, which were senescent.

The amounts of sodium and chloride in the leaves increased during leaf development, but when expressed relative to leaf water, the chloride concentration is remarkably constant in the mature leaves. Sodium concentration increased with age while potassium concentration fell.

(*b*) *Salt Regulation in* Aegialitis

The xylem sap of *Aegialitis* contained a higher concentration of chloride than that of *Rhizophora*; values ranged from 85 to 122 mN. A sample with 122 mN chloride contained 118 mN sodium and 14 mN potassium. Transpiration by a shoot of *Aegialitis* was about 1 ml per leaf per day, resulting in an input of about 100 μ-equiv. chloride per day to the leaf. Salt is removed from the leaf by glands on the upper surface.

TABLE 2

SALT CONTENT OF *AEGIALITIS* LEAVES

Values are means for five leaves; sample 1 was the youngest leaf in a sequence of increasing age

	Sample 1	Sample 2	Sample 3	Sample 4	Sample 5
Dry weight (g/leaf)	0·315	0·450	0·445	0·500	0·440
Water (% of fresh wt.)	72	60	60	59	60
Na^+ (μ-equiv/leaf)*	420(518)	325(480)	275(411)	280(388)	235(356)
K^+ (μ-equiv/leaf)*	155(191)	106(157)	87(130)	93(129)	70(106)
Cl^- (μ-equiv/leaf)*	415(512)	290(429)	270(405)	260(361)	255(386)
Mg^{2+} (μ-equiv/leaf)*	108(133)	330(488)	440(659)	590(819)	530(802)

* Mean concentrations (μ-equiv/ml of leaf water) in parentheses.

Table 2 shows the amount of salt in successive leaves on the shoot, compared with their dry weights. There is a decrease in sodium, potassium, and chloride content with age of leaf though dry weights are relatively constant for the older leaves. Clearly, a very large proportion of the salt taken up in the transpiration stream must be secreted by the salt glands.

Figure 1 shows the cumulative secretion of chloride in two leaves of area 28 and 32 cm^2. During the first day period the rate of secretion averaged 10 μ-equiv. per hour; over the night period it was 0·32 μ-equiv. per hour, and the following day 9·5 μ-equiv. per hour. On a leaf-area basis these values reduce to fluxes of 93, 3, and 88 p-equiv. cm^{-2} sec^{-1}.

In a further series of measurements, the mean noon secretion was 83 ± 15 (16), and the mean midnight secretion $5 \pm 0{\cdot}5$ p-equiv. cm^{-2} sec^{-1}, in mature leaves. This

difference is larger than could be accounted for by the difference in day and night temperatures. By means of these glands a typical leaf is able to remove about 100 μ-equiv. of salt per day.

(*c*) *Content of the Secretion from* Aegialitis *Glands*

Leaves cut from the tree will continue to secrete salt if their petioles are in water or a salt solution. Measurements of salt secretion under oil (Scholander *et al.* 1962) were made with cut stems in 20, 100, or 200 mM sodium chloride. The salt content of secretion under oil by leaves on the tree was also measured. Some of these measurements are listed in Table 3. Three sets of cut leaves and one of leaves sampled directly from the tree had unusually low chloride contents (<0·1N) but the reasons for this variation are not known.

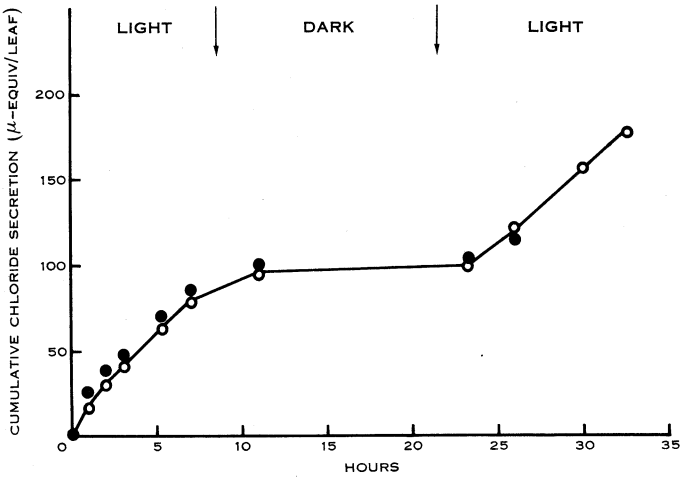

Fig. 1.—Cumulative secretion of chloride from the upper surface of *Aegialitis* leaves of area 28 cm^2 (○) and 32 cm^2 (●) on the tree in light and dark.

In further experiments it was found that there was agreement between observed chloride concentrations in the secretion and the chloride concentrations calculated from depression of freezing point by assuming the solution contained only monovalent chloride. Measurement of sodium and potassium concentrations confirmed that the secretion was predominantly sodium chloride. Means of four determinations were: chloride, 450 μ-equiv/ml; sodium, 355 μ-equiv/ml; potassium, 27 μ-equiv/ml.

The ratio of sodium to potassium in these exudates (13) is higher than in the leaves (3) of *Aegialitis* (Table 2) but closer to the ratio of about 8 in the xylem sap. However, this ratio differs from a previous estimate of 24–38 (Scholander *et al.* 1962). The reason for this difference is not known.

(*d*) *Secretion and Metabolism in* Aegialitis *Leaves*

(i) *Effect of Light.*—Table 4 gives rates of chloride secretion for two groups of *Aegialitis* leaves that were cut in darkness and kept in darkness or in artificial light

while the petioles were in 0·1M NaCl. The mean secretion in darkness was 10 times that observed with leaves on the tree in darkness [cf. Fig. 1 and Section III(*b*) above]. There was no significant difference between secretion rates of the group of cut leaves in darkness and in light.

(ii) *Effect of the Uncoupler CCCP on Secretion.*—The inhibitor carbonyl cyanide 3-chlorophenylhydrazone (CCCP) was fed through the petiole to cut leaves as a 50 μM solution in 100 mM NaCl, or applied to the surface of the leaf. The cut leaves

TABLE 3

CONCENTRATION OF CHLORIDE IN THE SECRETION FROM *AEGIALITIS* LEAF GLANDS, COMPARED WITH BALANCING PRESSURE AND MEAN ION CONTENT OF LEAVES

	Chloride Concn. (μ-equiv/ml)	Equiv. Osmotic Pressure (atm)	Balancing Pressure (atm)	Ion Content of Leaf (μ-equiv/g leaf water)		
				K^+	Na^+	Cl^-
Cut stems placed in:						
20 mM NaCl	720	32	—	83	340	262
	530	24	—	82	378	284
100 mM NaCl	480	21	—	—	—	560
	535	24	—	—	—	530
	450	20	—	—	—	370
	360	16	—	—	—	275
	—	—	16	—	—	—
	—	—	23	—	—	—
	340	15	14	107	241	45
	810	36				
	410	18	12	71	168	34
	340	15				
200 mM NaCl	400	18	—	105	438	75
	610	27	—	66	400	348
	630	28	—	70	364	268
Leaves on tree	1000	45	—	127	370	59
	1000	45	—	—	—	—
	910	41	—	90	342	275
	780	35	—	91	288	231
	—	—	47±1*	—	—	—

* Mean ± standard error of the mean of five samples from trees in bright sunlight.

were illuminated at a distance of 20 cm from a 40-W fluorescent lamp throughout the experiments. Table 5 shows that the CCCP inhibited secretion, but that there was a lag of about 2 hr between the time the inhibitor was applied and the reduction in secretion.

(*e*) *Distribution and Secretion of Infused Radioactive Chloride in* Aegialitis

Sodium chloride solution, labelled with ^{36}Cl was infused into a leaf through the petiole, which had been cut under 0·5M mannitol and kept in this solution for 12 hr.

Table 6 gives the specific activity of chloride in the secretion collected at intervals, and compares this with the specific activity of the sample infused and the chloride in several regions of the leaf. The final specific activity of the secretion was more than twice that of chloride in cells scraped from the upper surface of the leaf.

TABLE 4

SECRETION OF CHLORIDE BY CUT LEAVES OF *AEGIALITIS* IN LIGHT AND DARK

Values are means ± standard errors of the means for groups of six leaves placed in 0·1M NaCl in darkness or approximately 20 cm from a 40-W fluorescent lamp

Time	Secretion Rate (p-equiv. cm^{-2} sec^{-1})			
	Group A		Group B	
23·40–00·45	14 ± 5	Light	24 ± 5	Dark
00·45–07·35	62 ± 2		39 ± 9	
07·35–09·55	31 ± 11		37 ± 17	
09·55–17·05	15 ± 4		11 ± 3	Light

(*f*) *Structure of* Aegialitis *Salt Glands*

The glands, numbering about 900 per square centimetre, are found mainly on the upper surface of the leaf with a few on the lower surface. Each gland is situated in a depression of the epidermis and is about 30 μ in diameter. The structure of the glands as seen with the light microscope is shown in Plate 1, Figures 1–4. Light micro-

TABLE 5

INHIBITION OF SALT SECRETION IN *AEGIALITIS* LEAVES BY CARBONYL CYANIDE 3-CHLOROPHENYLHYDRAZONE (CCCP)

Hours after Treatment	Chloride Secretion (p-equiv. cm^{-2} sec^{-1})		
	Control	50 μM CCCP to Petiole	50 μM CCCP to Leaf
0–1	87	91	91
1–2	96	83	91
2–11·5	87	8	33
11·5–13·5	104	18	33

graphs of sections cut parallel to the surface of the leaf show that the upper part of the gland consists of three concentric rings of cells; serial sections indicate that there are usually eight cells in each ring. In transverse section (Plate 1, Fig. 3) the two inner rings of cells are shown to be elongate palisade-like cells, surrounded by smaller

cells of the outer ring. The gland is covered by a thick cuticle which penetrates the leaf between the gland and the epidermal cells (cf. also Plate 2, Fig. 1).

Electron micrographs of gland cells (Plates 2 and 3) show that there are considerable differences in the level of ultrastructural differentiation of the various cells in the gland. The palisade-like central cells have large vacuoles (the vacuoles contain some product that reacts strongly with the fixative giving electron-dense material) and only a small amount of cytoplasm. Nuclei seen in the light micrographs are also seen in the electron micrographs (Plate 2, Fig. 1).

TABLE 6

SPECIFIC ACTIVITY OF ^{36}Cl IN SECRETION OF CHLORIDE BY GLANDS OF *AEGIALITIS* LEAF

Secretion was collected at hourly intervals after transfer of cut leaf from 0·5M mannitol to 0·15 ml of 1·13M NaCl (89 mc ^{36}Cl/equiv. Cl^-). After 3 hr the leaf was transferred to water and at 5 hr leaf fractions were taken for analysis

Time (hr)	Cl^- Flux (p-equiv. $cm^{-2}\,sec^{-1}$)	^{36}Cl Flux (nc/hr)	Specific Activity (mc/equiv. Cl^-)	Specific Activity as a Percentage of Specific Activity Infused
0–1	14	19	10·2	11
1–2	69	54	5·9	7
2–3	88	290	24·8	28
3–4	89	365	31·0	35
4–5	85	407	36·0	40
Region of Leaf	**Cl^- in Samples from Leaf (μ-equiv/g fresh wt.)**	**^{36}Cl in Samples from Leaf (μc/g fresh wt.)**	**Specific Activity (mc/equiv. Cl^-)**	**Specific Activity as a Percentage of Specific Activity Infused**
Upper epidermis	418	6·9	16·4	18
Middle layer	476	9·1	19·3	22
Lower epidermis	418	10·8	25·6	29
Midrib	370	8·9	24·0	27

The basal cell (*BC*; Plate 2, Fig. 1) of the salt gland is thick-walled on two sides only, the other sides of the cell being covered by thickened cuticle that stains darkly on the inner surface. The cell contains many small vacuoles, some mitochondria, endoplasmic reticulum, and a nucleus. The endoplasmic reticulum in the cell was extremely dense and was associated with the cell wall (Plate 2, Fig. 2). This concentration of reticulum was similar to that found in the basal cell of the salt gland of *Avicennia marina* (West and Smith, unpublished data).

The sub-basal cells (*SBC*; Plate 2; Plate 3, Fig. 1) that join the basal cell of the gland to the palisade parenchyma leaf cells are also highly differentiated. They are characterized by their irregularly thickened cross walls (Plate 3, Fig. 1) and numerous plasmodesmata that pass through the walls joining these cells to each other and to the basal cell. The association of endoplasmic reticulum with the cell wall is shown in Plate 3, Figure 1. Many mitochondria are found in these sub-basal cells (Plate 2, Fig. 2) and serial sections indicate that they are concentrated in the region of the

plasmodesmata (Plate 2, Fig. 1). The plasmodesmata may contain membranes, since their contents stain strongly with lead citrate (Plate 2, Fig. 2).

The palisade mesophyll cells (*P*) which lie between the salt glands and the leaf veins are shown in Plate 1, Figure 3, and Plate 3, Figure 2. The cells are small with obvious vacuoles and with chloroplasts in the layer of cytoplasm (Plate 3, Figs. 2 and 3) which lines the cell wall. This layer of cells contains large intercellular spaces.

IV. Discussion

Although most of the sodium chloride of the marine environment is excluded by the root system of *Rhizophora* during uptake of water (for references to earlier work see Scholander *et al.* 1962, 1966) the results in Table 1 show a preferential retention of sodium in the older leaves of the growing *Rhizophora* shoot. The ratio of sodium to potassium increased from 2·5–3·6 in young leaves to 7–14 in mature leaves and the observed input of 17 μ-equiv. chloride per leaf per day does not lead to mean chloride concentrations greater than 600 μ-equiv/ml of leaf water (370 μ-equiv/ml in the youngest leaves, 550$\pm$10 μ-equiv/ml in older leaves; cf. Table 1). From this input and measured salt contents of leaves it is estimated that a mean growth rate of 3% increase in dry weight each day suffices to keep the chloride at the observed level.

The ratio of sodium to potassium in the younger leaves (2·5–3·6) is much lower than that in the older leaves (7–14). It seems that this apparent selective retention of sodium is in fact due to translocation of potassium out of the older to the younger leaves. In the present results (Table 1) the youngest, fully expanded leaf (No. 2 in Table 1) contains more potassium than the older leaves. Such a system of ion retranslocation certainly acts in other plant species (barley, mustard).

In contrast to the salt "excluder" *Rhizophora*, salt balance in *Aegialitis* is maintained mainly by secretion of salt from the glands on the leaves. These glands secrete predominantly sodium chloride, and consequently there is a build up of divalent cations in the leaf as it becomes older (Table 2). Magnesium in this example increased from about 100 μ-equiv. per leaf to just over 500 μ-equiv. per leaf. Another feature of salt regulation in *Aegialitis* due to secretion from these glands is the build up of a high level of potassium in the leaves relative to that of sodium (Na/K=3 in the leaves, about 8 in the xylem sap, and 50 in sea-water).

Collection of secretion under oil shows that water and salt move out of the leaves together. Measurements of balancing pressure made on other mangrove species growing in the intertidal zone showed that during the night it fell to about 25 atm (close to the osmotic pressure of sea-water) but during the day when transpiration started, it rose to nearly 50 atm. These values relate to the water potential in the leaf and hence the osmotic pressure of the secreted solution should be at least as large as the balancing pressure. Table 3 showed that there was in fact a reasonable agreement between osmotic pressure of the secretion (42$\pm$8 atm) and the balancing pressure (46$\pm$1 atm). Movement of water is maintained by the gradient of water potential resulting from secretion of salt; an analogous situation exists in many animal organs (e.g. gall bladder—Diamond 1962).

The salt-secretion mechanism of *Aegialitis* is one of the most active salt-secreting systems described in plants or animals. The secretion of chloride at 90 p-equiv. cm^{-2} sec^{-1} from *Aegialitis* leaves at noon corresponds to a chloride flux of about 5 n-equiv. cm^{-2} sec^{-1} over the total cross-section of the glands and about 25 n-equiv. cm^{-2} sec^{-1} if all the secretion is through the junction of the sub-basal cell and the annular space surrounding the gland (Plate 2, Fig. 1).

The 97% decrease in rate of secretion by *Aegialitis* leaves on the tree in darkness (Fig. 1) was confirmed by analyses on larger numbers of leaves over shorter periods in light and darkness [94% decrease, cf. Section II(*b*)] and is consistent with the earlier observation (Scholander *et al.* 1962) of a marked diurnal variation in chloride secretion by this species. The close association of chloride secretion rate to light intensity is not an obligatory feature of salt secretion in mangroves; Scholander *et al.* (1962) found that *Aegiceras corniculatum*, a species that secretes chloride at a similar rate to *Aegialitis annulata*, shows little diurnal variation in secretion rate. Further, it was observed that cut leaves kept in the dark with the petioles in 0·1M sodium chloride secreted chloride at more than half the rate observed with leaves on the tree in bright sunlight (Table 4). While there was a higher rate of chloride secretion in the dark by cut leaves than by leaves on the tree there was also a greater variability in secretion, and no significant difference could be shown between rates of secretion from cut leaves in light or dark (Table 4). The results provide no evidence for a direct coupling of the secretion mechanism to electron transport in chloroplasts, an observation consistent with the remoteness of cells with chloroplasts from the salt glands (cf. Plates 1, 2 and 3).

Carbonyl cyanide 3-chlorophenylhydrazone is an efficient "uncoupler" of energy-linked processes in mitochondria and chloroplasts (Heytler 1963) and when applied to the surfaces or cut petioles of leaves in 0·1M sodium chloride caused a marked inhibition of chloride secretion (Table 5). The delay in the effect may have been due to slow penetration to sensitive sites or to slow manifestation of a general interference with cell functions leading eventually to cell death. It is not known if this effect is a direct one on the coupling of electron transport to ion movement through biological membranes (e.g. of mitochondria in the sub-basal cells of the salt glands; cf. Plate 2, Fig. 2) or an indirect consequence of decreased supply of an essential metabolite or metabolites (e.g. ATP) through inhibition of its production.

In the experiment with ^{36}Cl to test the possibility that chloride passed directly to salt glands from leaf veins without complete equilibration with the main chloride pools of the leaf it was found (Table 6) that the specific activity of secreted chloride reached a value higher than the mean value found in any extensive region of the leaf, and more than twice that in the colourless epidermal cells scraped from the upper surface of the leaf. These cells had a lower specfic activity than any other region dissected from the leaf.

The electron micrographs of *Aegialitis* leaves show the presence of extensive intercellular spaces in the palisade layer of cells between the leaf veins and the salt glands (Plate 3, Fig. 2) and the observations reported here are consistent with an active transport system in the gland drawing salt from this region and competing

with salt-accumulation systems in other leaf cells. While it is not possible to define the position of the salt pumps more exactly it seems likely that the plasmodesmata and multivacuolate structure of the basal cells (Plate 2) could provide a trap to prevent back-diffusion as predicted by Scholander *et al.* (1962) by analogy with the convoluted tubule of animal sweat glands. The membrane system and mitochondrial layer at the outer wall of the sub-basal cells adjacent to the plasmodesmata are possible sites of active salt transport coupled to electron transport or hydrolysis of ATP or both. Discovery of the mechanism of the salt pumps in these glands awaits further investigation in which it is likely that the use of more selective inhibitors and more adequate histochemical methods will play a part.

V. Acknowledgments

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Explanation of Plates 1–3

Plate 1

Photomicrographs

Fig. 1.—Transverse section of a leaf of *Aegialitis* showing the glands (*G*) in the upper surface.

Fig. 2.—Section cut almost parallel to the leaf surface of *Aegialitis*; the four glands shown are sectioned at different levels.

Fig. 3.—Higher magnification of a leaf in transverse view. The gland is covered by a cuticle which penetrates between the gland cells and the leaf cells to approximately the level shown by the arrows. A leaf vein (*V*), epidermal cells (*E*), palisade mesophyll cells (*P*), and stomatal cavity (*SC*) are also shown.

Fig. 4.—As for Figure 2, but at a higher magnification. Stomata (*S*) also shown.

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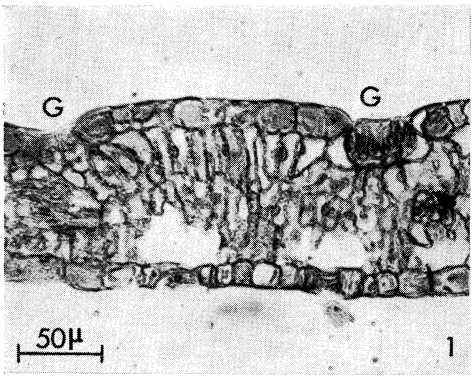

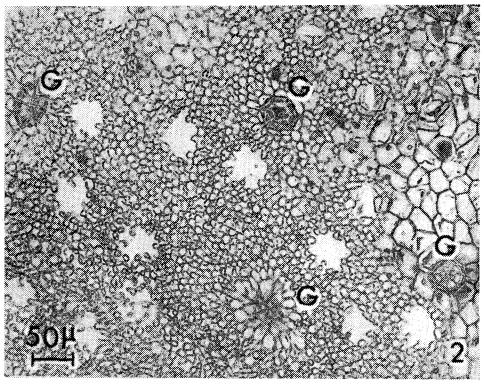

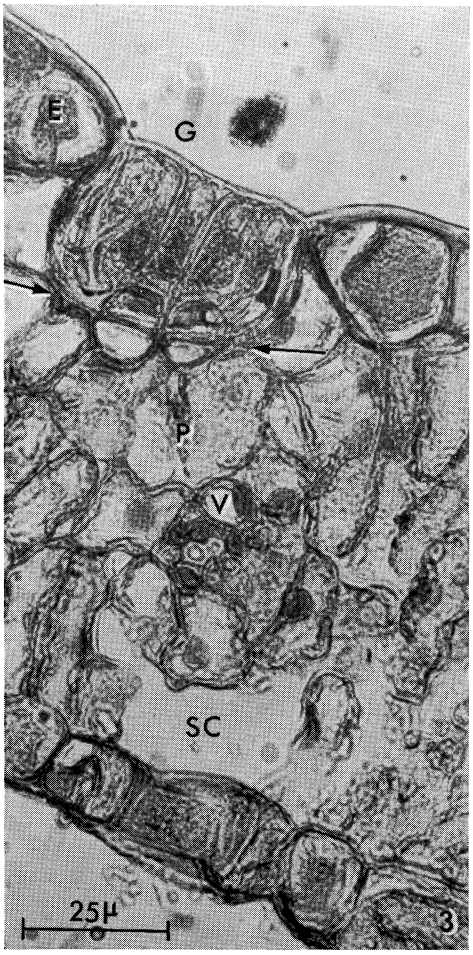

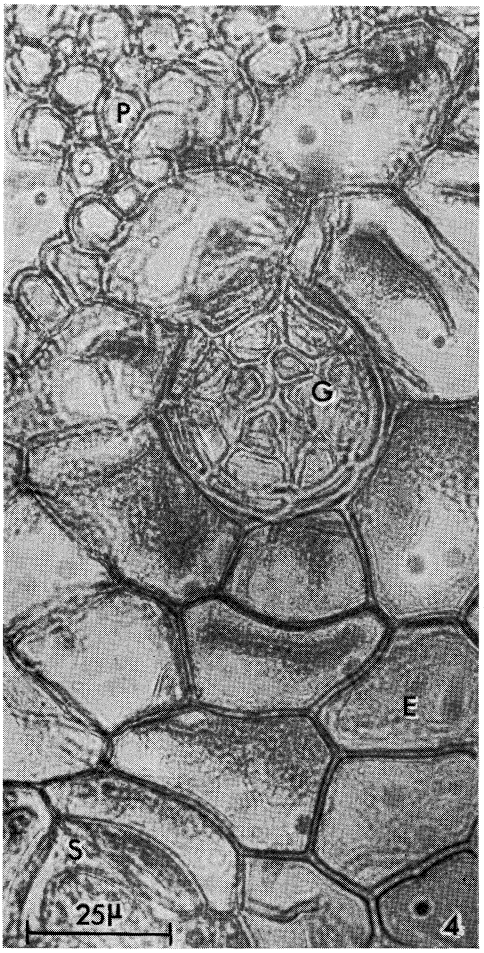

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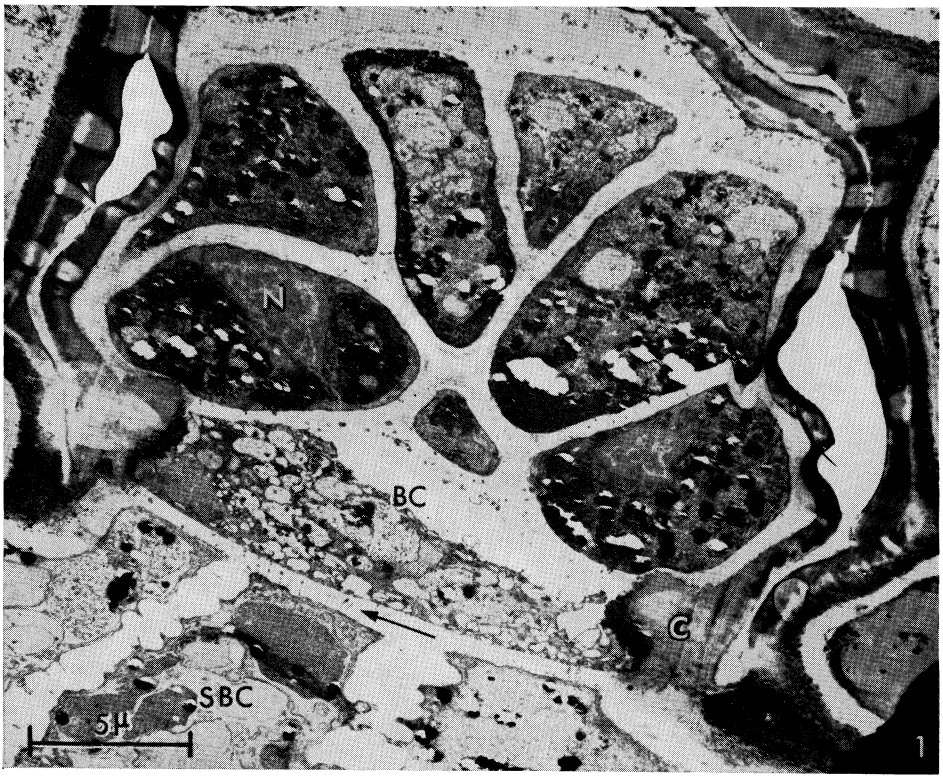
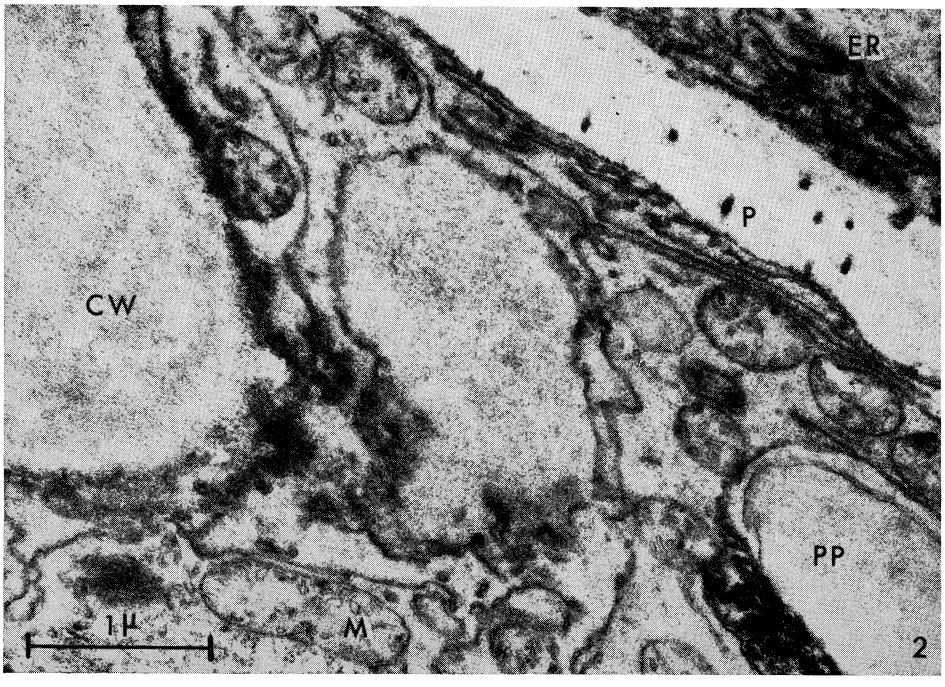
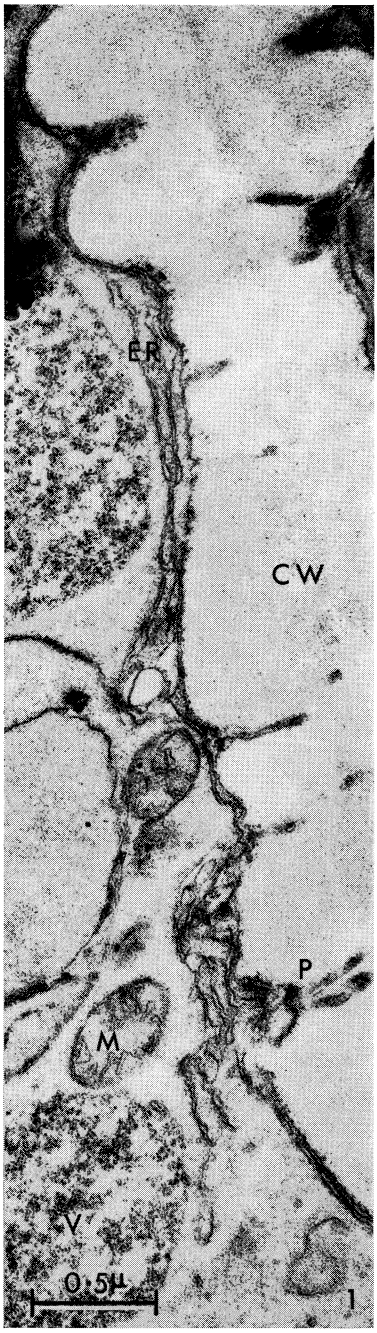
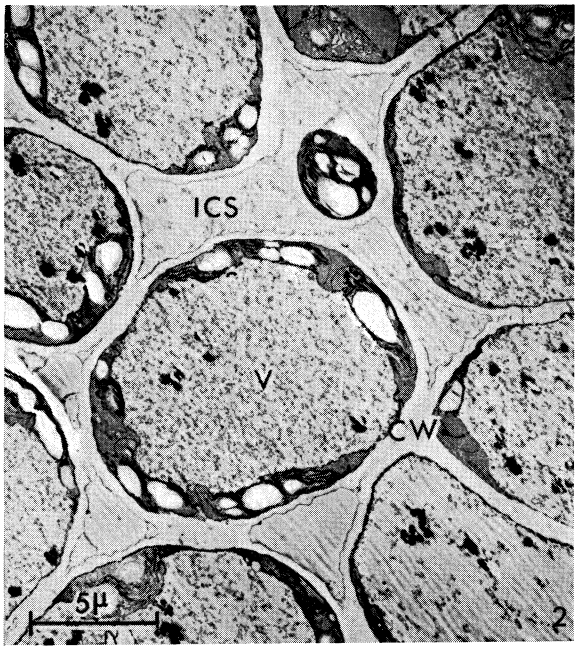




SALT REGULATION IN MANGROVES





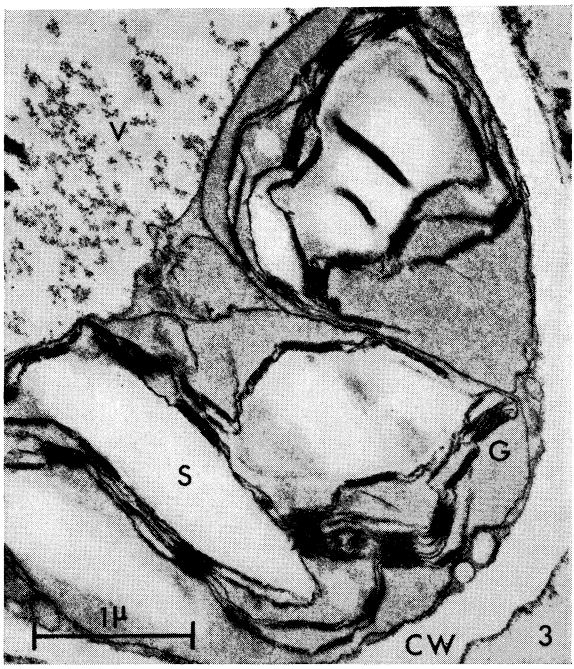


Plate 2

Electron micrographs

Fig. 1.—Electron micrograph of an oblique section through a gland. Seven cells of the gland are shown connected to the leaf cells by a highly vacuolate basal cell (*BC*). Sub-basal cells (*SBC*) with irregular walls and dense cytoplasmic contents are found below the vacuolate cell. Note the concentration of mitochondria and plasmodesmata in the area marked with the arrow. Cuticle (*C*) and nucleus (*N*) are shown.

Fig. 2.—An area from another gland similar to that marked by the arrow in Figure 1. Mitochondria (*M*), endoplasmic reticulum (*ER*), and protoplastids (*pp*) are concentrated in the sub-basal cell. There is a dense mass of endoplasmic reticulum near the wall in the upper connecting cell. Plasmodesmata (*p*) and a cell wall (*CW*) are also indicated.

Plate 3

Electron micrographs

Fig. 1.—Micrograph showing the irregularly thickened cell wall (*CW*) and associated endoplasmic reticulum (*ER*) from a sub-basal cell. The endoplasmic reticulum closely follows the outline of the cell wall while numerous plasmodesmata (*p*) also join the cells to each other. The vacuole (*V*) contains a dense granular deposit. *M*, mitochondria.

Fig. 2.—The palisade mesophyll cells that lie between the leaf veins and the gland. The intercellular spaces (*ICS*) are large and the cells are highly vacuolate (*V*).

Fig. 3.—Detail of a chloroplast from cells as in Figure 2. Starch grains (*S*) and well-developed grana (*G*) are clearly seen.