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Salt glands in flowering culms of *Eriochloa* species (Poaceae)

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ABSTRACT

Salt glands were found in *Eriochloa* (Paniceae-Poaceae): *E. montevidensis*, *E. pseudoacrotricha* and *E. punctata*. They occur on the culms, rachises and secondary ramifications of the inflorescence. The glands are bicellular structures with endodermal tissue at the base. They consist of a basal cell and an apical cell, which is a collecting chamber with a large pore at the top. It is proposed to conserve the term salt gland to designate excretory structures associated with endodermal collecting tissue. The elements present in the glands (detected by the use of X-ray micro-analysis) are: Na, Mg, P, S, Cl, K with an increase of the elements from the endodermal tissue to the cap cell. Because of energy needed to transport and excrete salts, salt glands are situated at the base of the inflorescence, which is the zone of maximal development of Kranz structure. It is inferred that *Eriochloa* is a facultative halophytic genus, derived recently from a halophytic ancestor.

UITTREKSEL

Soutkliere is aangetref by *Eriochloa* (Paniceae-Poaceae): *E. montevidensis*, *E. pseudoacrotricha* en *E. punctata*. Hulle kom voor op die halms, ragisse en sekondêre vertakkings van die bloeiwyse. Die kliere is tweesellige strukture met endodermale weefsel aan die basis. Hulle bestaan uit 'n basale sel en 'n apikale sel. Laasgenoemde is 'n versamelholte en het 'n groot porie op die punt. Daar word voorgestel dat die term soutklier slegs vir uitskeidstrukture geassosieer met endodermale versamelweefsel, gebruik word. Die elemente aanwesig in die kliere (opgespoor met behulp van X-straalmikroanalise) is: Na, Mg, P, S, Cl en K, met 'n toename in die elemente vanaf die endodermale weefsel na die mus-sel. As gevolg van energie wat vir vervoer en uitskeiding van soute benodig word, is soutkliere geleë aan die basis van die bloeiwyse, wat die streek van maksimale ontwikkeling van Kranz-struktuur is. Daar word afgelei dat *Eriochloa* 'n fakultatiewe halofitiese genus is en onlangs uit 'n halofitiese voorouer ontstaan het.

INTRODUCTION

Studies of the Kranz structure development in flowering culms of some species of *Eriochloa* (Arriaga 1990) revealed conspicuous structures in the transection. They correspond to secretory tissue (sensu Fahn 1979) and are salt glands.

Salts are continuously transported into plant shoots via the transpiration stream (Waisel *et al.* 1986). In plants growing in halophytic or semi-halophytic habitats, salt accumulation may eventually reach a hazardous level, and survival of plants may depend on reduction of the salt content of the shoot (Waisel 1972). Excretion of ions by specialized salt glands is a well-known mechanism for regulating the mineral content of the plant (Waisel 1972; Liphschitz *et al.* 1974).

Salt glands have been known and described for various plant species since the middle of the past century (Volkens 1884; Marloth 1887; Ruhland 1915; Sutherland & Eastwood 1916; Fahn 1979, 1988, 1990; Levering & Thomson 1971, 1972; Waisel 1972; Liphschitz *et al.* 1974; Liphschitz & Waisel 1974, 1982; Hong-bin *et al.* 1982; Oross & Thomson 1982; Waisel *et al.* 1986; Drennan *et al.* 1987, amongst others).

Salt glands have been described in 12 families of phanerogams (Liphschitz & Waisel 1982), and the Poaceae are unique in the monocotyledons in possessing these structures. Sixteen genera of the Chloridoideae and 17 of the Panicoideae have been shown to possess salt glands on both leaf surfaces (Liphschitz & Waisel 1982). In this work it is shown that salts glands occur in some species of *Eriochloa* and these epidermal appendages are described and illustrated. They occur on the culms, rachises and secondary ramifications of the inflorescence. Such glands present a new morphological type different from the graminoid salt glands previously described.

MATERIALS AND METHODS

Transverse sections of flowering culms were made from immediately below the inflorescence, the rachis and secondary ramifications. Both herbarium and fresh material was used. The herbarium material was restored and reconstituted by slow imbibition in warm water from 24 to 48 hours or in etanol-glycerol 1:1 from 48 to 72 hours. Sections were obtained either freehand or the material was embedded in wax and sectioned on a rotary microtome (for ontogenic studies). The sections were stained with Alcian Blue and Safranin (Cutler 1978) or Cresyl Violet (Dizeo de Strittmatter 1980).

Fluorescence microscopy was used for sections of herbarium material. On the basis of the results of Dizeo de Strittmatter (1986) and using Acridin Orange and Methylene Blue as fluorochromes in simple fluorochrome techniques and Acridin Orange-calcofluor in a combined technique, we were able to deduce the nature of the wall of the salt gland cells. Specimens were examined with a Zeiss fluorescence photomicroscope incorporating a high-pressure mercury vapor lamp HBO 50W, a BP 450-490 Blue exciter filter, a chromatic divisor FT 510 and a suppressing filter LP520.

Histochemical reactions were used to determine the nature of ions excreted from the glands. The presence of

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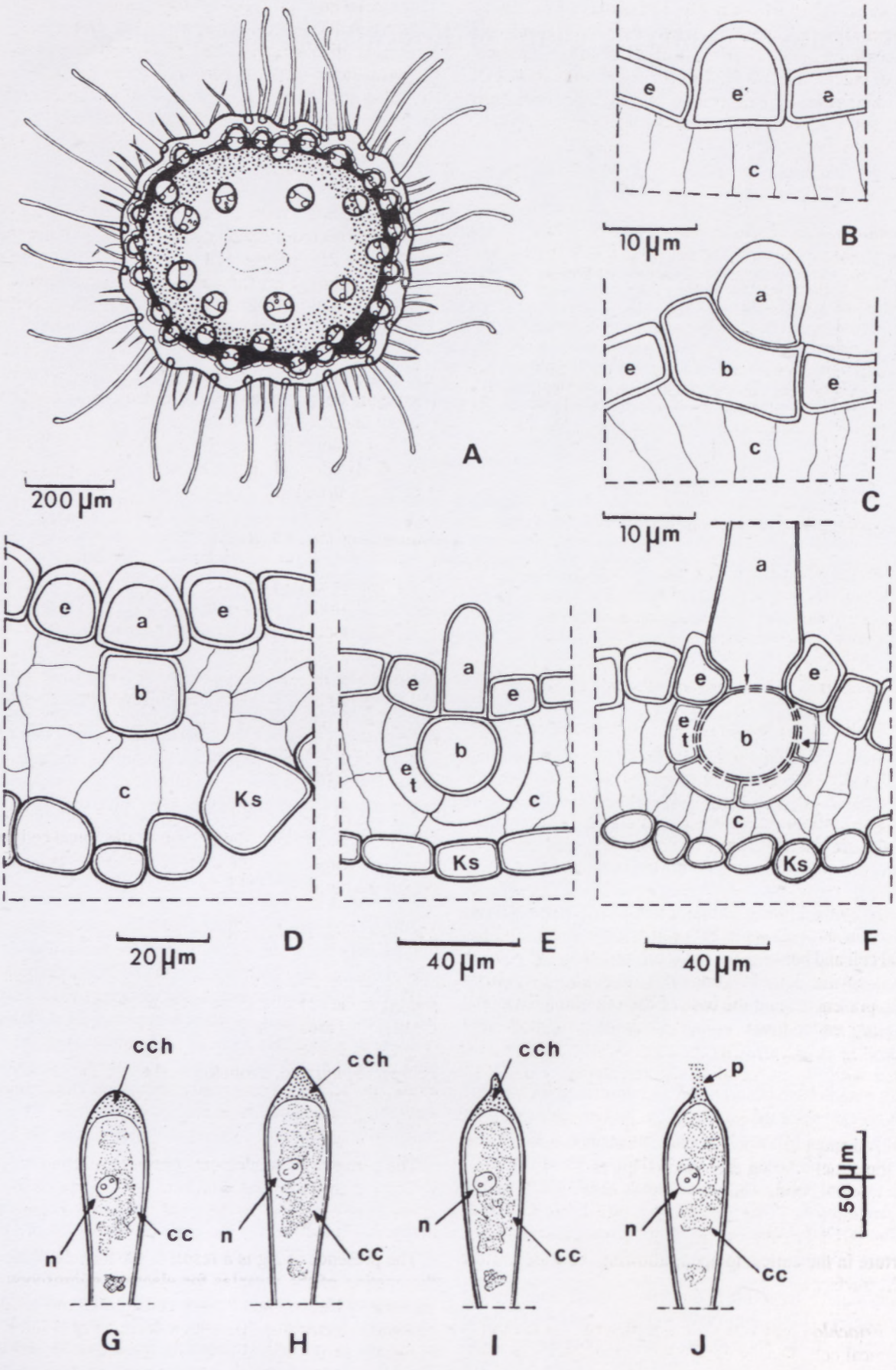

FIGURE 1.—A, *Eriochloa pseudoacrotricha, Saravia Toledo 1310*, t.s. of flowering culm of *Eriochloa* below inflorescence. B–F, *E. montevidensis, Pire s.n.*, ontogeny of salt gland: B, epidermal cell initiating differentiation; C, basal and apical cell formation; D, basal cell sunken beneath epidermal level, note also Kranz sheath; E, apical cell growing, shows differentiation of chlorenchyma surrounding basal cell to form endodermal tissue; F, mature salt gland, apical cell broken, endodermal tissue present with cutinization on cell walls and with pits connecting endodermal tissue with basal cell and this with apical cell. G–J, *E. punctata, Arriaga 584*, mature apical cell. a, apical cell; b, basal cell; c, chlorenchyma; cc, cytoplasm, denser in apex; cch, collecting chamber; e, epidermal cell; e', epidermal mother cell of salt gland; et, endodermal tissue; ks, Kranz sheath; n, nucleus; p, pore. Arrows show connection between cells.

Na was investigated using the technique described by Johansen (1940). The nature of the ions was also analysed and measured by X-ray micro-analysis in unfixed transections of culms, using a Phillips 515 SEM with an EDAX 9100 attachment. Photomicrographs were taken with Zeiss equipment and the schematic drawings were made with a Wild camera lucida.

Material examined

Eriochloa montevidensis

Baez 39 (BAB); *Saravia et al. 10072c* (CTES); *Venturi 702* (BA); fresh material: *Pire s.n.* cultivated Fac. Agronomía, UNRosario.

E. pseudoacrotricha

Lahitte & Castro 47614 (BAB); *Saravia Toledo 1310* (BA).

E. punctata

Ahumada 2570 (CTES); *Arriaga 312 & 576* (BA); *BA 61301*; *BAB 68290*; *Burkart 26145* (SI); *Cordini 106* (SI); *Pensiero 147* (SF); *Ragonese 3188* (SF); *Rodriguez 449* (BA); *Vegetti 442* (SF); fresh material: *Pire s.n.* cultivated Fac. Agronomía, UNRosario; *Arriaga 584* (BA).

RESULTS

Anatomical description of the salt glands

Culm transections of *Eriochloa* revealed a zone of excretory tissue near the base of the inflorescence. These epidermal appendages are much bigger than the macrohairs usually present in this genus (Figures 1A; 2A, B). These appendages consist of bicellular hairs associated with specialized cells at the base (Figures 1E, F; 2D, E).

These bicellular structures have a rounded basal cell, 35–45 μm in length, sunken into the chlorenchyma, and an elongated apical cell, 700–750 μm in length. The two cells meet at the level of the epidermal cells (Figure 1F). The walls of both cells are heavily cutinized (Figures 1F; 2D) and are distinct from the surrounding chlorenchyma tissue.

Numerous pit-like interruptions, and plasmodesmata are present in the cell walls between the basal cell and the apical cell and between the basal cell and the neighbouring chlorenchyma cells (Figures 1F; 2D). The specialized tissue present around the base of the salt gland is termed excretory endodermis, collecting tissue or endodermal tissue (Figure 1E, F). The endodermal tissue is not connected with the surrounding chlorenchyma by pits.

The distal part of the elongate apical cell is heavily cutinized and a subcuticular space forms between the wall and the cuticle during excretion (Figures 1G–J; 2F–H). This is a collecting chamber (Oross *et al.* 1985) where salt solutions accumulate. As the hydrostatic pressure within this compartment increases, it causes the pore aperture in the cuticle to open, allowing the fluid to flow to the surface.

In *Eriochloa* only one pore was observed at the top of the apical cell. During excretion a large drop is exuded. The increase in hydrostatic pressure in the collecting chamber initially causes the protrusion of the cuticula of the apex into a narrow structure resembling a finger, at the top of which the pore appears (Figures 1J; 2G, H). Obtuse and blunt but pointed (Lindley 1951) apices are therefore found in the distal cells of the salt glands in *Eriochloa* (Figure 2A–C).

Both basal and apical cells possess dense and granulose contents, and very conspicuous nuclei. The apical cell nucleus is displaced to the apical region where the cytoplasmatic contents are denser (Figures 1G–J; 2F–H). The basal and the apical cells, as well as those forming the endodermal tissue, are living cells with heavy cutinization of their walls. There is no direct connection between the salt glands and the vascular bundles.

The basal cell seems to function as a transport cell, whereas the excretion itself occurs at the apex of the apical cell (Figure 2H). These salt glands are present on the flowering culms, near the base of the inflorescence, on the rachis and the secondary ramifications. They were not observed on any other part of these plants.

These glands can be differentiated from the common macrohairs because they are more than 700 μm long and are associated with endodermal tissue at their base. Ordinary macrohairs are 125–250 μm long and are without endodermal tissue at their base, they are also unicellular structures.

Ontogeny of the salt glands

Salt glands are derived from an epidermal cell (Figure 1B), which divides periclinally to form two cells (Figure 1C). The inner cell sinks into the chlorenchyma during growth and differentiation (Figure 1D). It becomes rounded and its walls begin to be cutinized. The upper cell elongates and its walls are thickened by cutinization (Figure 1E). The walls of the neighbouring cells of the chlorenchyma surrounding the basal cell also become cutinized (Figure 1E, F).

The nuclei of the basal and apical cells become more and more conspicuous, the nucleus of the apical cell shifts towards the apex, and the cytoplasmic contents becomes denser and granulose (Figure 1G–J).

X-ray analysis of the contents of the salt glands

By running on a scanner line from the endodermal tissue up to the apical cell we determined by X-ray images the nature of ions present and their concentration gradients (Figure 3) in samples of flowering culms (*Pire s.n.*) of *Eriochloa punctata*. From the analysis of the graphics we conclude that: Na, K, Mg, P, S, Cl, are present, with K, and Cl the dominant elements.

The percentages of elements present are listed in Table I. Organic anions, nitrate and carbonate might be present as well but could not be detected by the microanalyser.

The presence of Ag is a result of the technique used in the coating of the samples for electron microscopy. An increase of Na, Mg and P from endodermal cell to apical cell was detected together with a decrease of S and K. Cl increases in the apical cell and decreases in endodermal tissue. The presence of Na in these salt glands was also confirmed by the use of the technique described in Johansen (1940).

The chemical nature of the thickening of the walls of the apical, basal and endodermal cells was investigated by the use of fluorescence microscopy. This thickening

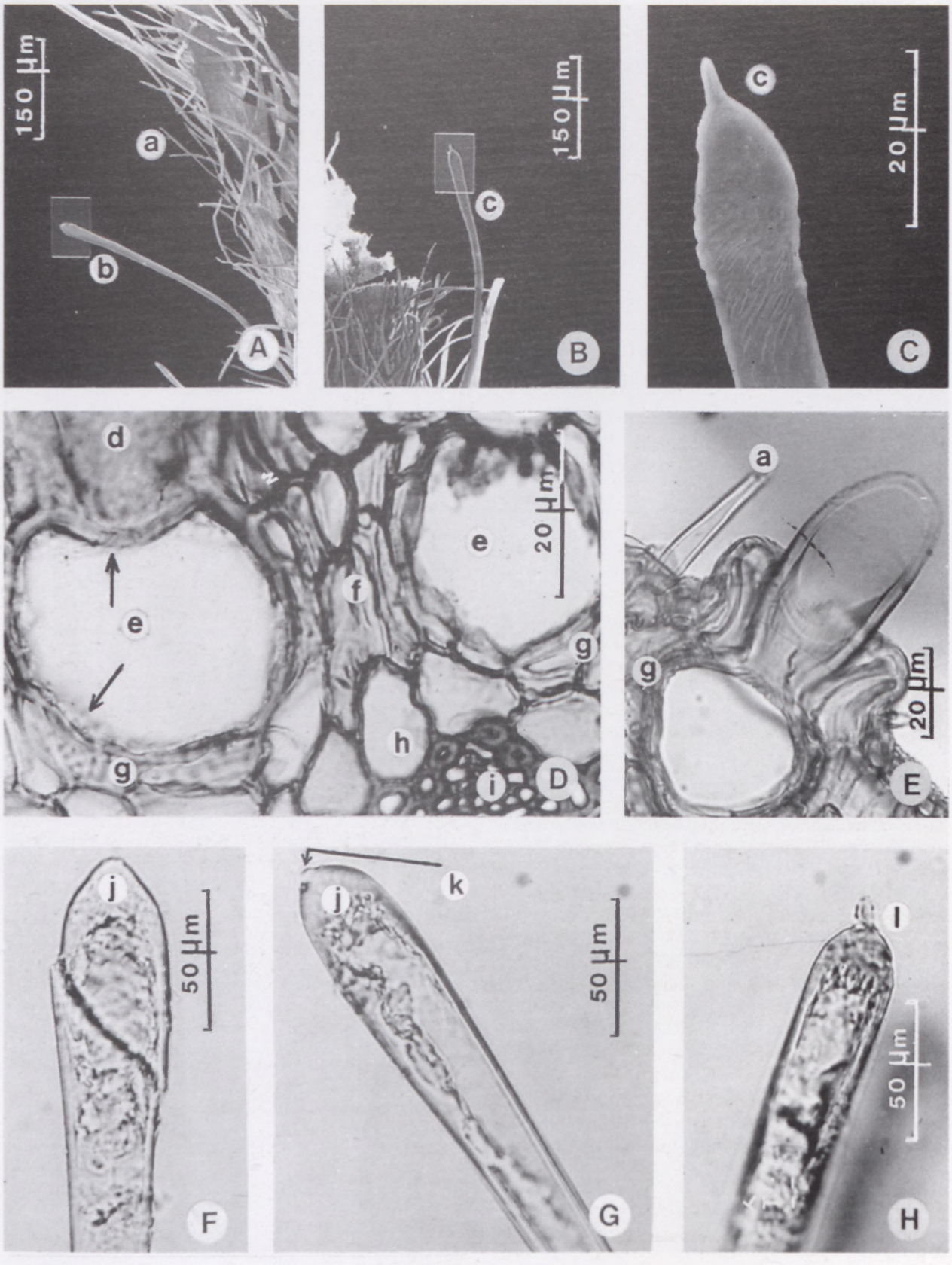

FIGURE 2.—A–C: *Eriochloa punctata, Pire s.n.*: A,B, SEM view of flowering culm below the inflorescence; C, SEM view of obtuse apex with acumen from a salt gland. D–H, LM views: D, basal cell surrounded by endodermal tissue and chlorenchyma; E, salt gland in an intermediate state of development with apical cell growing and endodermal tissue forming; F, G, H, distal zone of apical cell. a, macrohair; b, salt gland with obtuse apex; c, salt gland with a pointed apex; d, apical cell; e, basal cell; f, chlorenchyma; g, endodermal tissue; h, Kranz sheath; i, vascular bundle; j, collecting chamber; k, pore; l, pore excreting. Arrows show connection between cells. D, *E. punctata, BA 6130l*; E, *E. montevidensis, Venturi 702*; F–H, *E. punctata, Arriaga 584*.

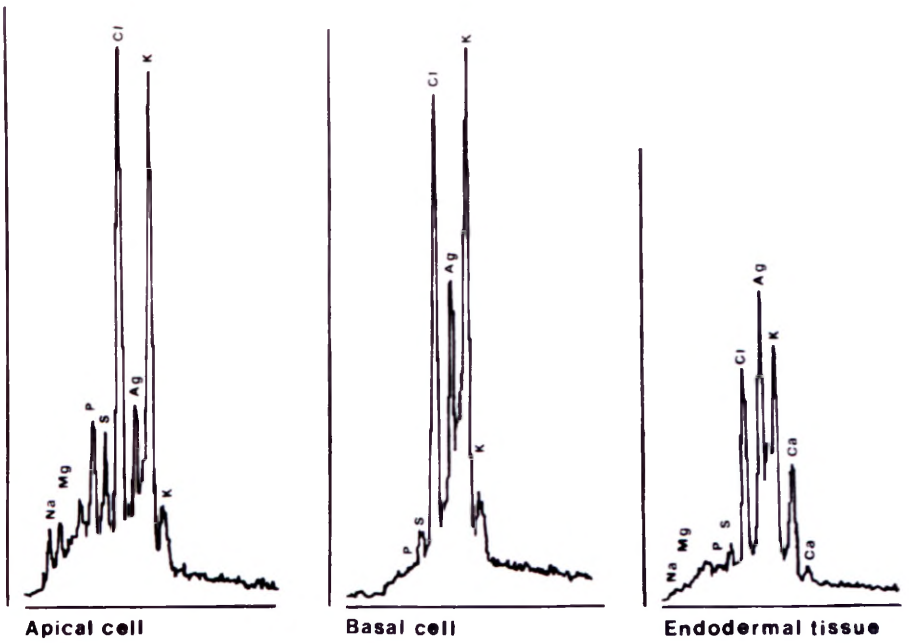

FIGURE 3.—Energy dispersive X-ray diagrams of the analysis of a salt gland.

results from the presence of cutin in the wall, with more cutinization in the base and distal zone of the apical cell.

DISCUSSION

The structure of salt glands varies greatly in different plant species but is usually similar in plants of the same genus or even within a family (Waisel 1972; Liphschitz *et al.* 1974). Based on their structural organization, there are three types of salt glands (Thomson 1975; Fahn 1979, 1988, 1990): the two-celled glands of the grasses, the bladder cells of the Chenopodiaceae and the multicellular glands which occur in other dicotyledonous families. The salt glands described for some species of *Eriochloa* do not coincide with the morphological type described for the Poaceae. Despite being bicellular structures they resemble a macrohair and not a typical microhair. They possess endodermal tissue at the base which is thought to prevent the flow of the excreted substances back into the plant. When the endodermal tissue is differentiated, it is structurally closer to that of the salt glands described for dicotyledons.

Retaining the original terminology of Waisel (1972) and Fahn (1979), it is proposed to restrict the term salt gland to the excretory structures associated with collecting tissues (i.e. endodermal tissue) and to reserve the term salt hairs (or salt pumps) for the excreting microhairs known in grasses.

Three fundamental features determine the effectiveness of salt glands in removing excess salt: a, their structure, location and abundance; b, their mechanism; c, their physiological and ecological significance (Waisel 1972). The basal cell of the salt hairs of grasses is sunken into the epidermis, located above it, or in intermediate positions. By contrast, the basal cell of the salt glands of *Eriochloa* is completely sunken into the chlorenchyma. As seen from data presented in Liphschitz & Waisel (1982) the more sunken the gland, the higher its excretion efficiency. Furthermore, a close relationship can also be found between excretion efficiency and basal cell dimensions. This suggests that the salt glands of *Eriochloa* are very efficient in excreting as they have a big, round basal cell completely sunken into the culm.

Spartina foliosa (Levering & Thomson 1971) and *Spartina anglica* (Hong-bin *et al.* 1982) have no cuticular layer separating the mesophyll from the salt hair. In *Eriochloa* the walls of the endodermal tissue are cutinized, as are the walls of the basal and apical cells.

At the apex of salt glands, between the cellulose layer of the wall and the cuticle, a subcuticular space is formed during excretion (collecting chamber). When pressure reaches a certain value, pores in the cuticle open, and droplets appear on the surface (Oross *et al.* 1985; Fahn 1990). In *Eriochloa* salt glands, a collecting chamber is visible at the top of the apical cell, but only one large pore is developed.

Within the Poaceae, in the Chloridoideae, ultrastructural studies of these two-celled structures have only been reported for three genera: *Spartina* (Levering & Thomson 1971, 1972), *Cynodon* (Oross & Thomson 1982) and *Distichlis* (Oross & Thomson 1982; Oross *et al.* 1985).

Although genera of the Panicoideae with excretory activity have been reported, these microhairs lack partitioning membranes in their basal cells (Amarasinghe & Watson 1988). Ultrastructural studies are required to determine whether *Eriochloa* species have these plasmalemma invaginations.

TABLE 1.—Percentages of elements present in salt glands

Element	Endodermal cell	Basal cell	Apical cell
Na	2.99%	none detected*	6.85%
Mg	1.29%	none detected*	3.95%
P	2.21%	0.84%	6.75%
S	5.02%	3.33%	4.48%
Cl	31.33%	38.30%	33.24%
K	57.16%	57.52%	44.77%

* too low to be measured.

Despite the fact that salt glands are best known on epidermal surfaces of leaf blades, they can sometimes be observed on epidermal surfaces of lemmas, paleas and lodicules. This is the first report of salt glands on the culms, as well as the rachis and secondary ramifications of Poaceae.

From this study it is not possible to indicate how excreted substances flow to the exterior. But it can be inferred in the light of Fahn's (1988) statement that these substances are excreted symplastically. Fahn (1988) pointed out the presence of complete cutinization of the walls on cells of the salt glands and endodermal tissue which 'indicates that the flow of excretory substances or their precursors takes place exclusively through the symplast and that flow of the excreted substances back into the plant through the apoplast is prevented'.

Ions reported as occurring in the excreted solutions of salt glands are: Na^+, K^+, Mg^{++}, Ca^{++}, Cl^-, $SO_4^=$, NO_3^-, $PO_4^=$ and HCO_3^- (Waisel *et al.* 1986; Fahn 1988). It was possible to analyse and measure ions present in the cap cell, the basal cell and in cells from the endodermal tissues in *Eriochloa punctata* by the use of an X-ray micro-analyser. The elements present were: Na, Mg, P, S, Cl, K, with a general increase of the elements from the endodermal tissue to the cap cell.

It is known that salinity induces changes in leaf anatomy increasing its leaf thickness and generally reducing photosynthesis and lowering the resistance to CO_2 intake (Longstreth & Nobel 1979), but no leaf succulence was observed in the *Eriochloa* species studied.

A possible relationship between photosynthesis and excretion is suggested by the work of Hill & Hill (1973). They proposed that ATP derived from respiration and possible cyclic photophosphorylation in the light is utilized in the excretion process. Since the glands do not have chloroplasts, the authors suggested that in the light the ATP would be derived from the mesophyll and diffuse symplastically to the glands. Moreover salts are transported outward, against a concentration gradient, by specific mechanisms which consume metabolic energy (Waisel 1972).

The siting of salt glands in *Eriochloa*, on culms at the base of the inflorescence, in rachis and secondary ramifications, coincides with the zone of maximal development of Kranz structure (Arriaga 1990), (zone of maximal efficiency in photosynthesis also), and would correspond to a need for high amounts of energy to transport and excrete salts by salt glands.

Salt glands in *Eriochloa* are derived directly from epidermal tissue and occur with other externally similar emergences such as 'normal' macrohairs. Patterson (1982) argues that homologous structures cannot occur in the same organism, so the glands cannot be homologous with the macrohairs. The same criterion was used by Linder *et al.* 1990 in connection with *Pentachistis* glands and other epidermal emergences.

The salt glands described here are excretory organs typical of many non-succulent halophytic species (Liphschitz & Waisel 1974). Some glands appear in species that today occupy rather non-saline environments. Excretion occurs in such plants only when they are transferred from the glycophytic to the semihalophytic or halophytic habitat (Liphschitz & Waisel 1982). In other plant species addition of salt to the growth medium affected the number of glands (Rosema *et al.* 1977). Although *Eriochloa* is not considered to be a halophytic genus, plants of this genus sometimes live in saline environments or saline patches, sometimes cohabiting with halophytic genera (i.e. *Distichlis*).

Eriochloa is a C_4 genus (Brown 1977; Ellis 1977; Hattersley 1982; Watson *et al.* 1986; Sánchez & Arriaga 1990). Many C_4 plants have been shown to tolerate Na and they frequently seem to be either halophytes or of halophytic origin (Liphschitz & Waisel 1974). The primary adaptation of C_4 plants was probably to saline environments (Laetsch 1974).

The existence of salt glands in a species which at present occupies non-saline habitats indicates that it probably originated as a halophyte and that, sometime in the past, its ancestors occupied saline habitats (Liphschitz *et al.* 1974). Though some species remained in saline habitats, most species migrated later from saline to non-saline habitats. Such migration probably occurred not too long ago, as those plants still retain many characteristics of their halophytic ancestors (Liphschitz & Waisel 1982). The existence of semisunken glands in plants which presently occupy non-saline habitats also suggests that the change from a halophytic to a glycophytic character, occurred only recently (Liphschitz & Waisel 1974). From all the points discussed above we infer that *Eriochloa* derives from a halophytic ancestor and is of recent origin.

Liphschitz & Waisel (1982) are of the opinion that species belonging to the Panicoideae and Chloridoideae have evolved from closely related ancestors which occupied saline (coastal?) habitats. The occurrence of salt glands (salt hairs) in 18 genera of Chloridoideae (Liphschitz & Waisel 1982; Taleisnik & Anton 1988; Marcum & Murdock 1990), with only three of them belonging to genera presently occupying saline habitats, and in 18 genera of Panicoideae, all of them at present occupying non-saline habitats, would lend support to this hypothesis.

It is obvious that salt glands in *Eriochloa* allow it to behave as a facultative halophytic genus, establishing it as an important candidate for economic utilization of saline environments.

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