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Salt Glands of some Halophytes in Egypt

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With 2 Figures

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Summary

SALAMA F. M., EL-NAGGAR S. M. & RAMADAN T. 1999. Salt glands of some halophytes in Egypt. – Phyton (Horn Austria) 39 (1): 91–105, 2 figures. – English with German summary.

Twelve species of salt excreting halophytes were collected from the salt marshes along the Red Sea (arid) and the west Mediterranean (semi-arid) coasts in Egypt. Those species belonged to seven genera and six families. The data revealed that the structure of the salt glands varied greatly among the investigated taxa and can be categorized in five groups. These groups are the vesiculated hairs or bladders of *Chenopodiaceae*; glands of *Tamaricaceae* and *Frankeniaceae*; glands of *Plumbaginaceae*; glands of *Avicennia marina* and glands of *Aeluropus lagopoides*. The results revealed also that the excreted salts are mostly composed of NaCl, but with more or less selectivity among different species. The composition of other ions varied also according to the different species.

Zusammenfassung

SALAMA F. M., EL-NAGGAR S. M. & RAMADAN T. 1999. Salzdrüsen einiger Halophyten aus Ägypten. – Phyton (Horn, Austria) 39 (1): 91–105, 2 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Zwölf Arten salzausscheidender Halophyten wurden in den Salzsümpfen am Roten Meer (arid) und an der ägyptischen Küste des Westmittelmeeres (semiarid) gesammelt. Die Arten gehörten 7 Gattungen und 6 Familien an. Die Ergebnisse zeigten, daß die Strukturen der Salzdrüsen innerhalb der untersuchten Taxa stark

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variieren und in 5 Gruppen eingeteilt werden können: aufgetriebene Haare oder Blasen bei den *Chenopodiaceae*, Drüsen bei den *Tamaricaceae* und *Frankeniaceae*, Drüsen bei den *Plumbaginaceae*, Drüsen bei *Avicennia marina* und Drüsen bei *Aeluropus lagopoides*. Die Ergebnisse zeigten auch, daß das ausgeschiedene Salz überwiegend aus NaCl besteht, aber mehr oder weniger stark innerhalb der einzelnen Arten. Die Zusammensetzung aus anderen Ionen schwankte ebenfalls entsprechend der einzelnen Arten.

Introduction

Halophytes are recognizably plants which survive high concentrations of electrolytes in their environments. Terrestrial halophytes can survive and complete their life cycles at optimum salt concentrations of 1.2–30 g/L salt in their rooting medium (SHANNON & al. 1994). In Egypt, halophytes occupy inland salt marshes (in the desert area) and littoral salt marshes (along the Mediterranean and Red Sea coasts). The Egyptian flora in account comprises about 2300 species; out of these there are almost 80 terrestrial halophytic species belonging to 31 genera and 17 families. Salt excreting halophytes are represented by about 30 species (BATANOUNY & ABO SITTA 1977). ZAHRAN 1982 classified 38 halophytic communities in Egypt into: 11 succulents, 13 excretives and 14 cumulatives. However, salt excreting plants have a reasonable representation in the Egyptian halophytes.

The function and structure of salt glands has been reviewed (HILL & HILL 1976, LIPHSCHITZ & WAISEL 1982, THOMSON 1975, THOMSON & al. 1988). FAHN 1988 classified the salt glands into two types: 1- glands eliminating salts into the vacuole of the bladder cell of the trichomes such as *Atriplex* spp.; 2- glands eliminating salts to the outside of the cells such as in *Limonium*, *Tamarix* and *Avicennia*. The structure of salt glands of *Atriplex* spp. was studied by OSMOND & al. 1969 and THOMSON & PLATT-ALOIA 1979; *Tamarix aphylla* by THOMSON & LIU 1967, SHIMONY & FAHN 1968 and BOSABALIDIS & THOMSON 1984; *Avicennia marina* by WALTER & STEINER 1937, CHAPMAN 1944, SHIMONY & al. 1973 and DRENNAN & al. 1987; *Frankenia* by THOMSON 1975 and CAMPBELL & THOMSON 1976. The structural and functional aspects of salt glands of different genera of family *Plumbaginaceae*, especially *Limonium*, were studied by ARISZ & al. 1955, ZIEGLER & LÜTTGE 1966, 1967, HILL & HILL 1973, FARADAY & THOMSON 1986a, b&c, VASSILYEV & STEPANOVA 1990 and BATANOUNY & al. 1992. The salt glands of *Limoniastrum monopetalum* were studied by BATANOUNY & ABO SITTA 1977.

Analysis of the excretion products of salt glands have been early studied. All these studies indicated that a variety of mineral salts are excreted but the major salt is NaCl (SCHTSCHERBACK 1910, HABERLANDT 1914, RUHLAND 1915, ARISZ & al. 1955, ARISZ 1956, HELDER 1956 and HAGEMEYER & WAISEL 1988). Analysis of salts excreted by *Tamarix* (WAISEL 1961, BERRY & THOMSON 1967, and BERRY 1970) and *Aeluropus* (POLLAK & WAISEL 1970) have shown that the excretion contained other ions including K, Ca, and Mg.

The present work aimed to study the structure of salt glands and the composition of excreted salts in some salt excreting halophytes growing in the arid (Red Sea coast) and semiarid (Mediterranean coast) regions. The effect of the environmental conditions on the glands and their excretion was also considered.

Materials and Methods

The present study was carried out on twelve species representing the most common salt excreting halophytes in Egypt. Those species belong to seven genera and six families namely: *Atriplex halimus* L. & *A. farinosa* Forssk. *(Chenopodiaceae)*; *Tamarix nilotica* (Ehernb.) Bge., *T. aphylla* (L.) H. Karst., *T. amplexicaulis* Ehernb. & *T. passerinoides* Delile *(Tamaricaceae)*; *Frankenia revoluta* Forssk. *(Frankeniaceae)*; *Limonium axillare* (Forssk.) O. Kuntze, *L. pruinosum* (L.) O. Kuntze & *Limoniastrum monopetalum* (L.) Boiss. *(Plumbaginaceae)*; *Avicennia marina* (Forssk.) Viern. *(Avicenniaceae)*; and *Aeluropus lagopoides* (L.) Trin. *(Poaceae)*. Specimens from the studied taxa were collected from the salt marshes along the Red and west Mediterranean Sea coasts, identified according to TÄCKHOLM 1974, and deposited at the Herbarium of the Botany Department, Assiut University. Duplicate specimens were also deposited at the Herbarium of Botany Department, Cairo University.

Specimens of leaves and stems were freshly taken in the field from young branches and immediately fixed and preserved in 70% ethanol. In the laboratory, the specimens were transferred to a fresh preservative solution. Segments of the leaves or stems were then dehydrated with graded ethanol, cleared in xylol and embedded in paraffin wax. Serial sections were cut in principal plane at approximately 5 to 7 µm thick. Sections were mounted in clean slides and deparaffinized thrice in xylol for 9 minutes (3 minutes interval), followed by absolute ethanol for 5 minutes. The sections were then double-stained with safranin and light green for light microscopic observations (SASS 1951), and were photographed on Kodak TMAX 100 film.

Salt crystals were collected in the field from the aerial portion of each species at different sites if possible along the Red and Mediterranean Sea coasts. If collection of salts was difficult, it was carried out by washing the salts into vials with distilled water. The solution was then evaporated in an oven at 105°C, resulting in precipitation of the salts. In all samples, 50 or 100 mg of salts were dissolved in 25 ml distilled water for analysis of salt composition.

Sodium and potassium were determined by Carl-Zeiss Flame Photometer. Calcium and Magnesium were determined by Atomic Absorption/Flame-Emission Spectrophotometer (Shimadzu-model AA-630-02). Chloride was measured by titration method as described by JACKSON 1958. Nitrate was determined by using Bausch and Lomb Spectronic 2000 colorimeter after reduction to nitrate according to a method modified by LARESSON & al. 1989 from KAMPHAKE & al. 1967. Sulphate was determined as $BaSO_4$ according to BLACK & al. 1965. Phosphate was estimated by the molybdate blue color method described by VOGLER 1965.

Results

A- General description of salt glands in the studied species:

The present results reveal that the structure of salt glands varies greatly among the investigated taxa, and can be categorized in five groups:

Vesiculated hairs or bladders

These hairs or bladders are represented in *Atriplex farinosa* and *A. halimus* of *Chenopodiaceae* and consist of a large highly vecuolated bladder cell attached to a narrow stalk (Fig. 1 A, B). This stalk consists of one to three cells according to the age of the hairs, therefore the vesicles are either short- or long-stalked, and consequently the bladders appear as stratified entities on the leaf surfaces. The vesiculated hairs are completely covered by cutinized layer. This layer is thicker on stalk cell(s) than on the bladder cell. It is also observed that *Atriplex farinosa*, inhabiting the more arid region of the Red Sea coast has a higher density of the vasiculated hairs than *A. halimus* which inhabits the semi arid region of the Mediterranean coast.

Glands of *Tamaricaceae* and *Frankeniaceae*:

The salt glands of the four studied species of *Tamaricaceae*: *T. aphylla, T. nilotica, T. passerinoides* and *T. amplexicaulis;* and *Frankenia revoluta* consist of eight cells (Fig. 1 C–F). Six of these cells are characterized by their dense cytoplasm, large nucleus and numerous very small vacuoles. These cells are known as the excretory cells, and appear to be arranged in three pairs: the outer, the middle and the inner pair (Fig. 1 D). The other two cells are characterized by large central vacuoles and are known as the inner vacuolated collecting cells. A cuticular layer encloses all of these cells except for little portions of the walls between the collecting cells and the innermost excretory cells. The uncuticularized areas of the walls are known as transfusion zones. However, the only communication between the mesophyll and excretory cells is by way of the collecting cells and through these transfusion zones. The salt glands of the above five species are distributed on both sides of leaves as well as on the surfaces of the stems. These glands are sunk in groves and wells under the epidermal level. In *Frankenia revoluta*, the glands on the adaxial side of the leaf are particularly distributed among simple or compound hairs.

Glands of the *Plumbaginaceae*:

In spite of the fact that the structure of salt glands varies greatly among the different species it may be very similar in plants of the same genus or even within the same family as in the case of *Plumbaginaceae*. The structure of the salt glands of *Limonium axillare, L. pruinosum* and *Limoniastrum monopetalum* is basically the same in cellular arrangement and number of the cells (Fig. 2 A, B, C). These glands are composed of a complex of sixteen excretory cells and large four sub-basal collecting cells. These excretory cells arrange in four circles. The four central excretory cells or the first circle are accompanied at their outer sides by smaller ad-

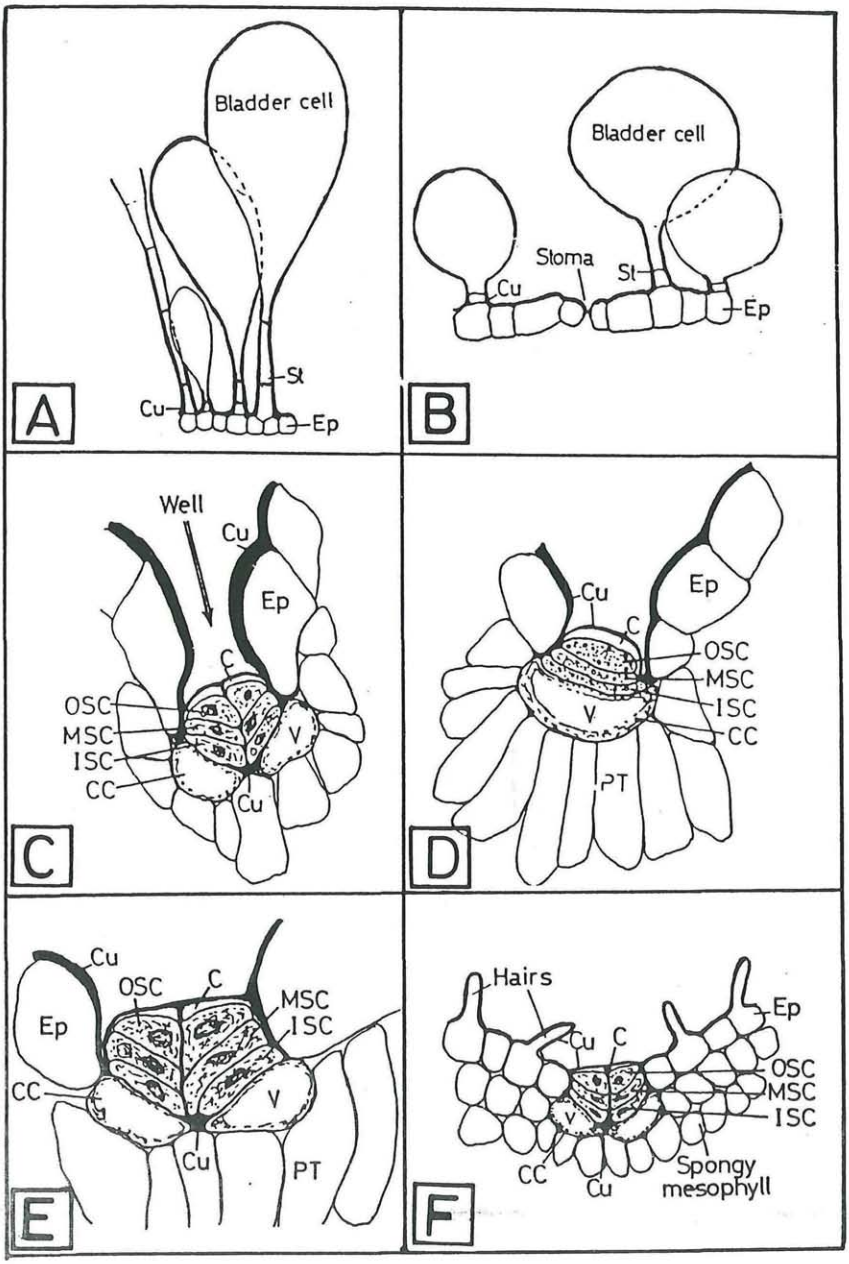

Fig. 1. Schematic drawing of vesiculated hairs of *Atriplex farinosa* (A) and *A. halimus* (B); and salt glands of *Tamarix nilotica* (C), *T. passerinoides* (D), and *Frankenia revoluta* (E & F).

joining or accessory cells of the second circle. Both circles are surrounded by two other cup-shaped layers, the outer and the inner layer, each of them consisting of four cells. These glands are sunk into the epidermis except those on stems of *L. pruinosum*, which are located individually on the top of a special elevated cortical structure.

Glands of *Avicennia marina*:

The salt glands of *Avicennia marina* consist of 2 to 4 collecting cells, one disc-like stalk cell and 4 to 8 radially arranged excretory cells (Fig. 2 D, E). The excretory and stalk cells contain numerous minute vacuoles and dense cytoplasm, while the collecting cells have large central vacuoles. The outer walls of stalk cells and excretory cells are covered by a cutinized layer separated from the outer walls of the excretory cells thus creating a large collecting compartment. This collecting compartment appears as a transparent cavity. These glands are present on both surfaces of the leaves. On the adaxial side these glands are sunk in densely distributed crypts. On the abaxial side the glands protrude above the leaf surface and distributed among the non-glandular hairs (Fig. 2 E). On this side, there are some glands which differ from the others and consist of one collecting cell, two disc-like stalk cells (in two layers) and four excretory cells. The non-glandular hairs consist of three to four cells. The upper most cell becomes markedly flattened in laminar plane, whereas the subterminal cells elongate in the opposite plane.

Glands of *Aeluropus lagopoides*:

The salt glands of *Aeluropus lagopoides* consist of only two cells: a small outer cap cell situated on a nick-like protrusion of a large basal cell (Fig. 2 F). This cap cell as well as the neck-like protrusion of the basal cell contain a dense cytoplasm, while the underlying part of the basal cell has a large vacuole. The external surface of the cap cell and the upper part of the basal cell is covered by a thick cutinized layer. This layer is distended and becomes detached from the wall forming a very small cavity or collecting compartment. These glands are located on both adaxial and abaxial sides in longitudinal furrows between the leaf veins. The furrows or grooves are created by revolution of the leaf margins toward the upper surface, where numerous prickles are observed.

B-Composition of the excreted salts:

The compositions of the salts excreted by the epidermal glands of certain halophytes under investigation are shown in Table 1. The determinations were made only on samples which were collected from the parent plants in the field. In salts excreted by all the studied species, presence of phosphate, nitrate or nitrite was below the detection limit of the methods

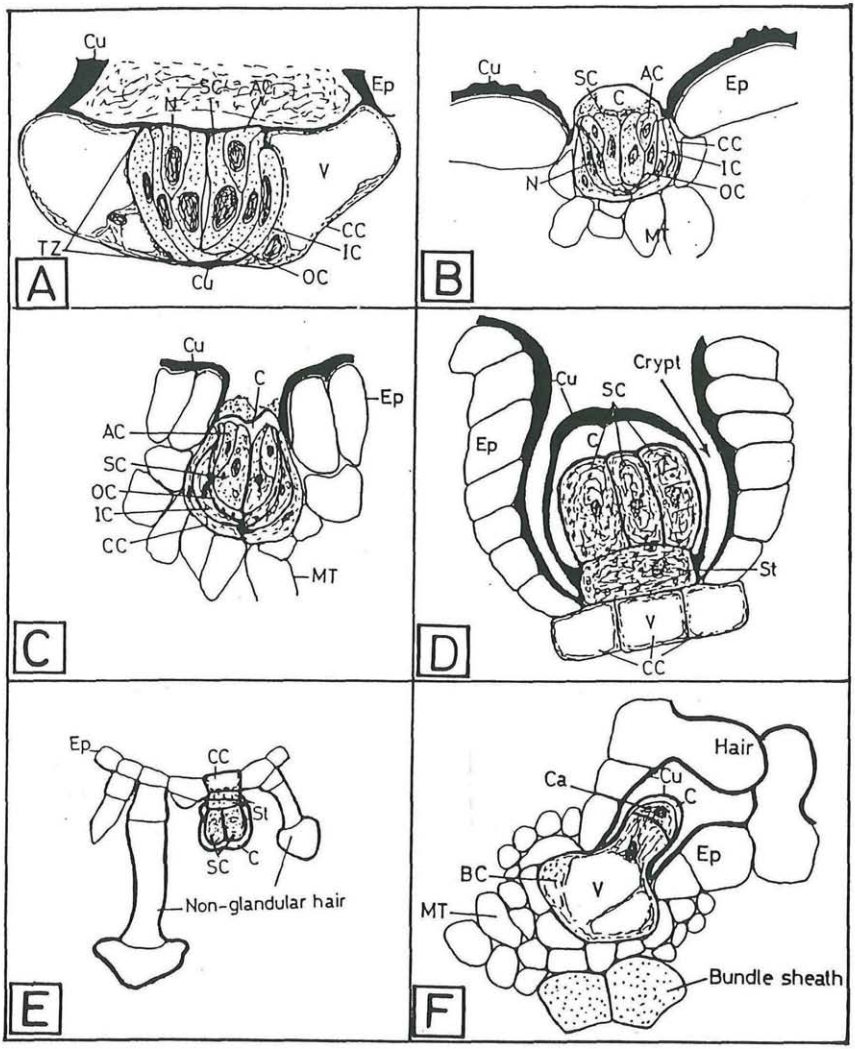

Fig. 2. Schematic drawing of salt glands of *Limoniastrum monopetalum* (A), *Limonium pruinosum* (B), *L. axillare* (C), *Avicennia marina* glands of the upper surface (D) and lower surface (E), and microhairs of *Aeluropus lagopoides* (F).

Abbreviations used in Figs. (1, 2).

AC – accessory cell
BC – basal cell
Ca – cap cell
CC – collecting cell
C – collecting compartment
Cu – cuticle
Ep – epidermis
IC – inner cup cell
ISC – inner secretory cell
MSC – middle secretory cell
Mt – mesophyll tissue
N – nucleus
OC – outer cup cell
OSC – outer secretory cell
PT – palisade tissue
SC – secretory cell
St – stalk cell
TZ – transfusion zone
V – central vacuole

Table 1.

Composition of the salts excreted by the epidermal glands of different halophytic species under field conditions. The values are the average percentages of the dry crystallized salts collected from each species at different sites ±SE. n = replicates; measurements are from different individuals.

Species	n	Na	K	Ca	Mg	Cl	SO4	Total	Others
Tamarix nilotica	8	40.17±0.38	1.50±0.20	1.35±0.20	0.54±0.07	46.86±0.80	5.30±0.61	95.73	4.27
T. aphylla	4	40.68±8.03	2.97±0.14	1.35±0.77	3.05±0.25	25.37±2.39	18.96±7.56	92.37	7.63
T. amplexicaulis	4	37.11±1.72	2.10±0.66	2.07±0.82	1.48±0.43	40.28±5.07	11.49±3.42	94.53	5.47
T. passerinoides	4	40.11±0.23	1.30±0.44	0.75±0.01	0.26±0.03	49.73±1.49	3.16±1.70	95.30	4.70
Frankenia revoluta	8	36.21±2.32	1.13±0.22	2.28±0.47	3.54±1.23	52.92±1.06	1.38±0.34	97.46	2.54
Limonium axillare	6	40.0±0.49	1.63±0.28	1.15±0.17	1.11±0.11	37.76±2.60	10.0±2.22	91.65	8.35
L. pruinosum	6	36.37±1.30	4.43±1.38	1.43±0.37	1.92±0.54	42.27±2.63	7.16±1.95	93.58	6.42
Limoniastrum monopetalum	8	29.89±3.86	0.47±0.10	2.22±0.58	3.82±1.24	43.47±2.37	5.52±2.71	85.40	14.60
Avicennia marina	10	44.10±0.23	0.41±0.06	0.50±0.07	0.28±0.04	53.61±0.29	0.63±0.02	99.53	0.47
Aeluropus lagopoides	4	40.95±0.55	1.79±0.43	1.06±0.35	0.74±0.09	51.06±0.30	1.31±0.09	96.91	3.09

used. The results revealed that NaCl is the most abundant salt excreted by glands of all species. It comprises more than 66% of the total weight of crystallized salts with some variation between different species.

In *Avicennia marina*, Na and Cl accounted for about 98% of excreted salts. Excretion of K, Ca and Mg collectively accounted for less than 1.2% of the crystallized salt. It is noted that the percentage of Cl alone exceeds that of mono- and divalent cations collectively. Composition of salts excreted by glands of *Tamarix* spp. show that NaCl is predominant and its percentage in *T. aphylla* is lower than in other species. The two major ions, Na and Cl, were represented by approximately 66, 77, 87 and 89% of the weight of salts excreted by *T. aphylla, T. amplexicaulis, T. nilotica* and *T. passerinoides*, respectively. Generally, the contribution of the Cl ion in the excreted salts was more than that of the Na ion. Contrariwise, the salt excreted by *T. aphylla* showed a higher percentage of Na than Cl. The divalent cations Ca and Mg and anion SO_4 were represented by relatively higher percentages in salts excreted by *T. aphylla* than by other species. In comparison with all studied species, the excreted salts of *T. aphylla* contain the highest proportion of SO_4 (about 18.9% of the total ions). The six ions, Na, K, Ca, Mg, Cl, and SO_4, account for between 92 and 96% of the total weight of salts excreted by *Tamarix* spp. However, there is a portion less than 7% of salts which was not detected. The majority of it seems to be carbonate and bicarbonate.

The composition of salts excreted by glands of both *Frankenia revoluta* and *Aeluropus lagopoides* shows more similarity with that excreted by *Avicennia marina*. More than half of the crystallized salts was Cl (51–53%), but the percentages of divalent cations were higher in salts excreted by *F. revoluta* than by two other species. However, NaCl is also the predominant salt excreted by glands of *F. revoluta* and *A. lagopoides*, contributing more than 89% of the total weight of salts. Data in Table 1 show that the excreted salts by the three species contained comparatively a very low proportion of SO_4. On the other hand, salt glands of the three species are characterized by the highest selectivity mechanism for Na and Cl over other ions.

In the salts excreted by the three species of family *Plumbaginaceae* (*Limonium axillare, L. pruinosum* and *Limoniastrum monopetalum*) the percentage of Na and Cl together ranged between 73 and 78% of the total ions. In *L. axillare*, Na represented with a higher percentage than Cl. Salts excreted by *Limoniastrum* were characterized by higher percentage of divalent cations Ca and Mg. Their contribution was about threefold that in *L. axillare* or *L. pruinosum*. Potassium is represented by less than 1.8% of the weight of salts. Sulphate comprised 5 to 10% of the total ions in salts excreted by the glands of the three species. The six ions constitute 85 to 93% of the total weight of excreted salts. However, there is an un-

determined portion ranging between 6 to 15% of the total weight of salts, which is probably considered as carbonate and bicarbonate.

Discussion

In the present study, data revealed that the two species, *Atriplex farinosa* and *A. halimus (Chenopodiaceae)* are shown to have a similar leaf anatomy. The vesiculated hairs consist of a large highly vacuolated bladder cell situated on top of a narrow, 1–3 celled stalk. The size of the bladders and the number of cells consisting the stalk differ according to the age of hairs. Growth of the bladder cell is accompanied by the formation and expansion of the central vacuole due to salt accumulation. Due to the differences in length, hairs appear as stratified entities collapsed on the leaf surfaces. They may function as heat insulator and reflector (Black 1954). On the other hand, this may explain the increasing density of epidermal hairs in case of *A. farinosa* compared to *A. halimus*: the former belonging to the more arid and saline regions of the Red Sea coast. However, it can be suggested that plants of the more arid and saline habitats develop dense bladder hairs. The submicroscopic structure of the stalk cell of the *Atriplex* hairs observed by Osmond & al. 1969 is strikingly similar to that of the excretory cell in multicellular salt glands. Analogous to the simplest type of glands in *Aeluropus*, the vasiculated hairs of *Atriplex* can be considered as salt glands, and the excreted salts remain trapped in the bladder cells.

From the taxonomic point of view, *Frankeniaceae* is a closely related family to *Tamaricaceae* so the salt glands of *Frankenia revoluta* appear to be similar to those of the four studied species of *Tamarix* (Fig. 1C, E, F). The glands of *Frankenia* are sunk in the epidermis of both leaf-sides. Those of *Tamarix* spp., especially on the stems, are located in well-like cylindrical depressions. The salt gland consists of eight cells. The six upper cells are the excretory cells whereas the two basal cells are the collecting cells. All the excretory cells are characterized by containing dense cytoplasm. In contrast, the collecting cells contain large central vacuoles. Each gland is in contact with the mesophyll cells which are arranged perpendicularly on the collecting cells (Fig 1 D). However, these findings are in agreement with the observations of Thomson & Liu 1967 and Shimony & Fahn 1968 on *Tamarix aphylla*. It is known that the salt gland in *Tamarix* or *Frankenia* is enclosed by a cuticular layer except in the two transfusion area between the collecting cells and the lower pair of excretory cells. The cuticle is separated from the walls of the excretory cells along the outer surface creating a collecting compartment. The present study revealed that this compartment appears to be separated into two cavities (one for each of the outer excretory cells) by extension of the cuticular layer inwards to the central anticlinal wall of the gland.

The structure of salt glands of *Limonium axillare, L. pruinosum* and *Limoniastrum monopetalum* are generally similar (Fig. 2A, B, C). FARADAY & THOMSON 1986a examined the salt glands of eleven species belonging to six different genera of the family *Plumbaginaceae*, and they found a similar ultrastructure in all species, suggesting that the salt glands of members of the family are extremely similar. The results indicated that the size and general morphology of the salt glands varied among the species examined. The glands of *L. axillare* and *Limoniastrum monopetalum* and also those on leaves of *L. pruinosum* are sunk into the epidermis. The glands on stems of the latter are not sunk, but are located individually on the top of a special elevated structure. This also was observed by WAISEL 1972 for the same species (*Statice pruinosa*). The glands of *Limoniastrum* are larger than those of other species, especially the collecting cells which are highly vacuolated (Fig 2A). The similarity in glands structure in members of the family Plumbaginaceae supports the suggestion of FARADAY & THOMSON 1986a. They suggested that the primary pathways and basic mechanisms of salt movement through the glands may be the same in all species of this family and hence for all salts excreted.

The results reveal that the leaves of *Avicennia marina* bear salt glands on both surfaces. On the adaxial side the salt-excreting glandular hairs are sunk in crypts; but on the abaxial side they occur above the surface and they are distributed among non-glandular hairs. The salt glands consist of an indefinite number of cells (7–13), while the non-glandular hairs consist of only three or four cells. This corresponds with the observations of CHAPMAN 1944 in *Avicennia nitida*, and also of FAHN & SHIMONY 1977 in *A. marina*. Furthermore, the latter authors suggested that both types of hairs are initiated and developed similarly up to the three-celled stage, but they did not give any reason why the non-glandular hairs developed only on the lower surface. According to our observations, it can be suggested that such structure is an important adaptive character. However, the position of salt-excreting glands sunk in crypts, wells and grooves or distributed among hairs or prickles, would increase the relative humidity directly around the glands and the excreted solution would not drop down rapidly after excretion. Therefore, such conditions are good for efficient excretion process, as sunk stomata do to decrease transpiration. On the other hand, the large number of excretory cells will amplify the excretory surface of the gland (DRENNAN & al. 1987).

Among the salt glands of different species studied, those of *Aeluropus lagopoides* are the simplest types, which are also known as microhairs. Their structure is exactly similar to those of *Aeluropus repens* and *A. litoralis* among twenty-five species belonging to the family Poaceae examined by LIPHSCHITZ & WAISEL 1974. Such bicellular microhairs occur mainly in almost all nonpooid grasses (AMARASINGHE & WATSON 1988,

AMARASINGHE 1990). It is worthy to mention that no direct connection exists between the gland cells and the vascular bundles, which are surrounded by "Kranz" structure of bundle sheath indicating that this species is a C_4-plant.

The results also reveal that the excreted salts are mostly composed of NaCl, but with more or less selectivity among different species. The two ions accounted for approximately 98% for *Aeluropus*; 87–90% for *T. nilotica*, *T. passerinoides* and *F. revoluta*; 77–79% for *T. amplexicaulis*, *L. axillare* and *L. pruinosum*. The lowest percentages of NaCl composition were recorded in salts excreted by *L. monopetalum* (73%) and *T. aphylla* (66%). The dry salt of the Red Sea water is found to be composed of approximately 55% Cl, 31% Na, 8% SO_4, 3.7% Mg, Ca < 1%, and K < 1%. In comparison, Cl alone constituted about 49 to 54% of salts excreted by *A. marina*, *F. revoluta*, *T. passerinoides* and *Aeluropus lagopoides*; and 25 to 47% in the other investigated species. In all species studied, Na constitutes 30 to 44% of the dry excreted salts. However, as Na and Cl are the predominant ions in natural saline soils along the sea shore, they are also the predominant ions excreted.

The composition of other ions in the excreted salts varied among the different species. The highest percentages of SO_4 were found in salts excreted by species of *Tamarix* and *Limonium*. The divalent cations Ca and Mg together were represented in salts excreted by *L. monopetalum* and *F. revoluta* with percentages higher than in other species. In contrast, Na was represented by the lowest percentages in salts excreted by these two species. On the other hand, when Na constitutes the majority of salts excreted, the other cations were represented with very low percentages (e.g. *Avicennia marina*). Therefore, the monovalent (K) and divalent cations (Ca & Mg) apparently inhibit sodium excretion. A similar behavior was observed in *Aeluropus litoralis* by POLLAK & WAISEL 1970 who found that excretion of Na was partially inhibited by K and Ca. Obviously, the ability to select ions varies from one species to another, and the order of preference of certain ions depends on the species itself (WAISEL 1972) as it is also a function of the composition of the root environment (BERRY & THOMSON 1967, BATANOUNY & al. 1992).

Calcium carbonate has been detected in salts excreted by many species, but it was not known whether carbonate is actually excreted by the glands (SAKAI 1974, BATANOUNY & ABO SITTA, 1977, BAUMEISTER & ZIFFUS 1981, SALAMA 1988), or precipitated due to reaction of the fluid with the atmospheric CO_2. BERRY 1970 reported that although bicarbonate was not added to the nutrient solution, it was found in large amounts in the salt excreted by glands of *T. aphylla*. The original idea that calcium carbonate is excreted by glands was skeptically dismissed (WAISEL 1972). Recently, WAISEL 1991 concluded that the highly alkaline aqueous film that cover the

twigs of *T. aphylla* constitutes an efficient trap for ambient CO_2 and preserves it mostly as bicarbonates and carbonates. In our investigation, the undetected portions of excreted salts that are regarded to be calcium carbonate were large in different species of families *Tamaricaceae* and *Plumbaginaceae*. According to WAISEL 1991, the precipitated carbonate is periodically redissolved, and the CO_2 released and subsequently absorbed and assimilated by the mesophyll. However, the glands in such different species, despite excretion of salts, function as a carbon-concentrating system.

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