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Anatomical leaf adaptations in vascular plants of a salt marsh in the Atacama Desert (Chile)

Adaptaciones anatómicas foliares en plantas vasculares de un pantano salobre en el Desierto de Atacama (Chile)

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ABSTRACT

A community of vascular plants living in a salt marsh in the Atacama Desert (northern Chile) was studied. Environmental parameters such as high solar radiation, drought, wind and high salt concentration are the most important limiting factors. Above-ground vegetative organs of twelve species living in this environment were morphologically and microscopically analyzed in terms of adaptive features that allow them to survive under these conditions.

These species showed an interesting display of traits such as extremely reduced leaf area, striated cuticles, sunken stomata, compact leaf tissues, salt crystals, salt glands and vertically oriented photosynthetic parenchyma. These characteristics were statistically tested in order to establish the clustering degree among them; two leaf patterns were found within the sample. The particular leaf anatomy exhibited is discussed, considering it as being adaptive to the stressful environmental conditions of the area.

Key words: Atacama Desert, salt marsh, leaf anatomy.

RESUMEN

Se analizaron las plantas vasculares que conforman una comunidad de pantano salino ubicada en el Desierto de Atacama. La alta radiación solar, sequedad atmosférica, viento y alta concentración salina son los factores limitantes para la sobrevivencia de estas especies. El análisis morfológico y microscópico de órganos vegetativos aéreos de doce especies dominantes de esta zona mostró interesantes características adaptativas, tales como: máxima reducción de área foliar, cutículas estriadas, estomas hundidos, compactación del mesófilo foliar, presencia de glándulas de sal y parénquima fotosintético orientado verticalmente. Estas fueron analizadas estadísticamente para determinar su grado de agregación, lográndose establecer de esta forma dos modelos foliares. La anatomía foliar descrita se discutió en relación a su significado adaptativo frente a las estresantes condiciones ambientales del área.

Palabras claves: Desierto de Atacama, pantano salino, anatomía foliar.

INTRODUCTION

Deserts are among the most hostile habitat for vascular plants because of their environment. Drought and high solar radiation plus the low water holding capacity of sandy soils challenge plants with problems in absorbing, conducting and storing water. Salt deserts add salinity to the above mentioned characteristics and this creates harsh conditions by causing extra difficulties in water absorption and salt metabolism and balance within the plant. Plants living in extremely dry habitat have been described as xerophytes (Maximov 1931) and they cope with water deficiency by decreasing their transpiration rates to a minimum. Salinity implies extra devices for maintaning an adequate osmotic potential and excreting excess sodium and chloride ions (Hansen *et al.*, 1976). Leaves, which are clue organs in transpiration and photosynthesis, become structurally altered in relation to the environment (Magnum 1950) thus,

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they should be suitably modified to inhabit a salt desert.

Anatomical leaf characteristics in relation to aridity have been described (Montenegro *et al.*, 1979, 1980, 1981, Turelli *et al.*, 1985, Mauseth 1988), and the most outstanding ones appear to be: leaf orientation, modified cuticles, reduced external leaf surface, high stomatal densities, compact leaf tissues and water storing devices. Foliar modifications related to high salinity have been reported by Black (1954), Mozafar & Goodin (1970), Franceschi & Horner (1980) and others, and they are best exemplified by salt excreting glands and salt crystals.

Our aim was to analyze the morphological traits of above-ground vegetative organs of plants living in a salt marsh in terms of adaptive features that allow them to survive in this particular environment.

MATERIAL AND METHODS

The study site is located in the Atacama Salt Desert (Salar de Atacama) at the Atacama Desert (23°23'S, 68°21'W) of Chile. The Atacama Salt Desert lies between the Cordillera de Los Andes and the Cordillera, de Domeyko at an altitude of 2.305 m (Fig. 1).

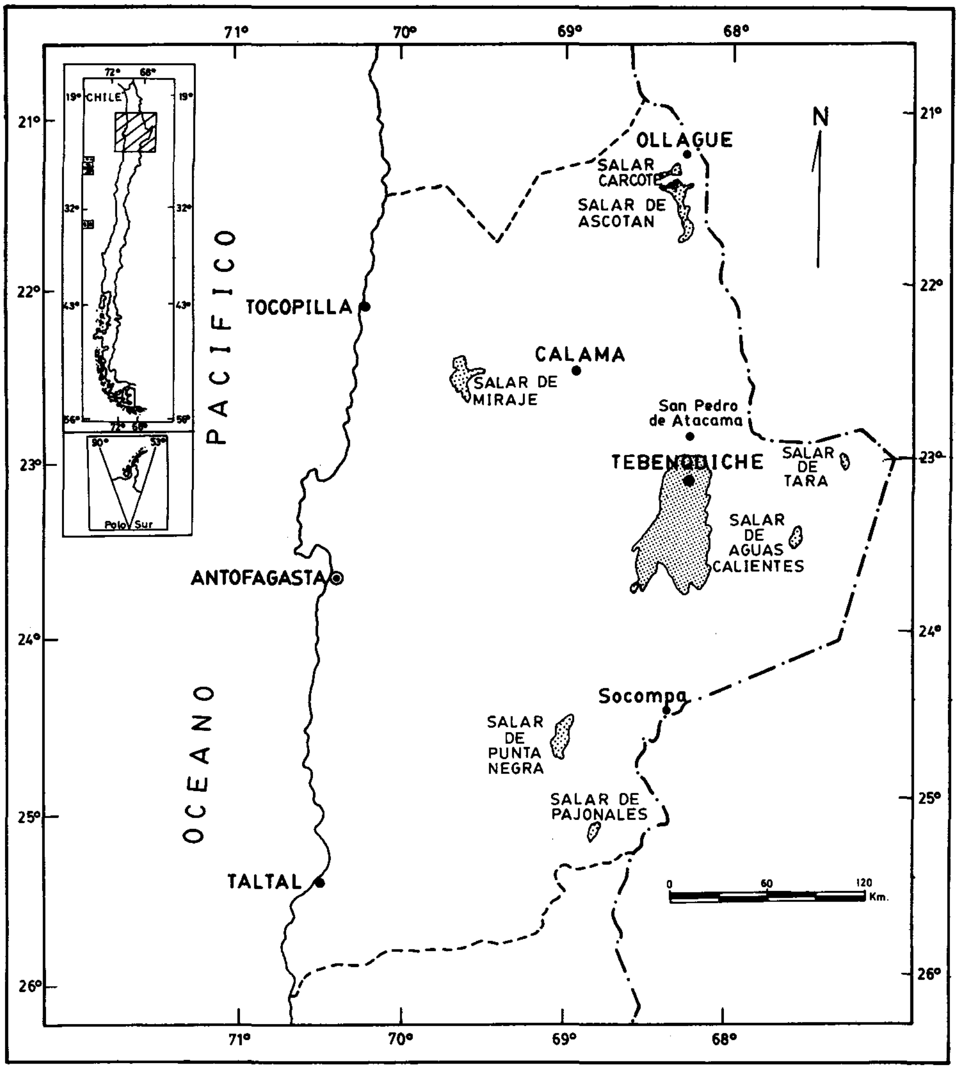


Fig. 1: Location of the study site in the Atacama Desert (northern Chile).

Ubicación del sitio de estudio en el desierto de Atacama (Norte de Chile).

The vegetation was sampled in Tebenquiche (23°08'S, 68°15'W), a shallow salt lake 70 cm average depth with a vascular plant community of low (10-50 cm) grass-like and succulent perennials extending about 60 m around the lake. The lake was characterized as hypersaline with 250 gr/l of salt, inhabited by *Artemia salina* by Zúñiga *et al.* (in press).

The climate is extremely dry with high solar radiation levels. Di Castri & Hajek (1976) describe it as tropical with precipitation occurring in summer months.

Most of the dominant species of the area were sampled and characterized by their life form (Table 1, Fig. 2). Nomenclature follows Marticorena & Quezada (1985) and Poblete (1989). Ten samples for each

TABLE 1

Name, family and growth form characteristics of the analyzed species (listed according to increasing plant size, matching numbers on drawings in Fig. 2). Nomenclature follows Marticorena & Quezada (1985) and Poblete (1989).

Nombre, familia y forma de crecimiento de las especies analizadas (presentadas en orden creciente de tamaño en concordia con los números de los dibujos de la Fig. 2). Nomenclatura según Marticorena y Quezada (1985) y Poblete (1989).

Species	Family	Life form
1. *Distichlis spicata*	Gramineae	Herbaceous, perennial, stoloniferous
2. *Lycium humile*	Solanaceae	Woody, perennial, suculent, stoloniferous
3. *Nitrophila atacamensis*	Chenopodiaceae	Herbaceous, perennial, succulent, deep rooted
4. *Festuca deserticola*	Gramineae	Herbaceous, perennial, erect, tufty
5. *Puccinellia frigida*	Gramineae	Herbaceous, perennial, erect, tufty
6. *Triglochin palustris*	Juncaginaceae	Herbaceous, perennial, leafless, stoloniferous
7. *Scirpus olneyi*	Cyperaceae	Herbaceous, perennial, leafless, stoloniferous
8. *Scirpus* sp.	Cyperaceae	Herbaceous, perennial, leafless, stoloniferous
9. *Sarcocornia fruticosa*	Chenopodiaceae	Herbaceous, perennial, succulent
10. *Juncus balticus*	Juncaceae	Herbaceous, perennial, stoloniferous
11. *Baccharis juncea*	Compositae	Herbaceous, perennial, stoloniferous
12. *Phragmites australis*	Gramineae	Herbaceous, perennial, vigorous, erect.

Fig. 2: Drawings of the sampled species in increasing size sequence. Code for species: 1.– *Distichlis spicata;* 2.– *Lycium humile;* 3.– *Nitrophila atacamensis;* 4.– *Festuca deserticola;* 5.– *Puccinellia frigida;* 6.– *Triglochin palustris;* 7.– *Scirpus olneyi;* 8.– *Scirpus* sp.; 9.– *Sarcocornia fruticosa;* 10.– *Juncus balticus;* 11.– *Baccharis juncea;* 12.– *Phragmites australis.*

Ilustraciones de las plantas muestreadas en orden de tamaño creciente: 1.– *Distichlis spicata;* 2.– *Lycium humile;* 3.– *Nitrophila atacamensis;* 4.– *Festuca deserticola;* 5.– *Puccinellia frigida;* 6.– *Triglochin palustris;* 7.– *Scirpus olneyi;* 8.– *Scirpus* sp.; 9.– *Sarcocornia fruticosa;* 10.– *Juncus balticus;* 11.– *Baccharis juncea;* 12.– *Phragmites australis.*

species were fixed in FAA. Leaves were embedded in Paraplast and stained in safranin and fast-green for histological analysis. SEM samples were dehydrated in an increasingly graded acetone series and dried from 100% acetone via CO_2 in a Polaron E 3,000 critical point drying apparatus. Then they were coated with a gold layer 100 A thick. Statistical analysis was done by Ward's Minimum Variance Cluster Analysis (SAS 1985).

RESULTS

The most relevant morphological traits were analyzed for all species (Tables 2 and 3) living in the area. All species shared the following characteristics: low aereal size, small leaf area, thick epidermis, thick cuticle, vertically oriented leaves and the absence of a spongy parenchyma. Sunken stomata were found in *Sarcocornia fruticosa* and *Baccharis juncea.* Other species like *Festuca deserticola* had folded leaves and *Puccinellia frigida* had wax rods covering guard cells. Water storing tissues occupied an important amount of total leaf volume in *Lycium humile* and *Sarcocornia fruticosa.* Different kinds of crystals appeared in *Lycium humile, Nitrophila atacamensis, Triglochin palustris, Sarcocornia fruticosa* and *Baccharis juncea*; salt glands were found in two of them (*Lycium humile* and *Distichlis spicata*) and Kranz anatomy occurred in only one (*Distichlis spicata*). Except from *Festuca deserticola* and *Juncus balticus* the rest of the species had modified cuticles (striations, wax rods, etc.) and only two of them (*Distichlis spicata* and *Festuca deserticola*) had a well developed set of trichomes. In analyzing these results, the following fact must be taken into consideration: in aphyllous species, the peripheral anatomy of their photosynthetic stem was considered to correspond in form and function to a leaf and it was analyzed as such in our discussion. *Sarcocornia fruticosa* which is apparently leaf-less presents all the structures of true leaves in the peripheral part of the stem thus it was considered as a leaf bearing species.

Statistical treatment was applied to all the species that presented true leaves. Ward's Minimum Variance Cluster Analysis showed two tendencies in leaf form (Fig. 3). One cluster (the upper one) was characterized by small, succulent unifacial leaves with thick epidermis, protected stomata, several layers of photosynthetic parenchyma, water storing parenchyma, centrally located veins and no air spaces. Crystals are abundant all through the mesophyll. The other cluster (the lower one) had bifacial leaves with thin folded blades, papilous epidermis, well developed and abundant bulliform cells, protected stomata, sclerenchyma in strands or layers and compact photosynthetic parenchyma.

DISCUSSION

The main physical factors faced by the sampled plants are drought, solar radiation, wind and high salt concentration. The relation between factors producing physical stress and the leaf anatomical trait is outlined in Table 4.

All sampled plants have small leaves (Table 2). This could be a response to drought, which produces high evapotranspiration rates which are lowered by reducing leaf area. This morphological trait produces a low external surface to volume ratio and enhances water conservation but, on the other hand, lowers the rate of CO_2 absorption (Mauseth 1988). Spongy parenchyma is not present in these plants; the mesophyll is surrounded by several layers of photosynthetic parenchyma (Fig. 4a). This tissue arrangement results in leaves with a low internal surface to volume ratio which produces a high resistance to water loss (Magnum 1950) and a lower ability to absorb CO_2 from the apoplast; as a final consequence, photosynthetic efficiency is impaired (Parkhurst 1982).

C_4 photosynthetic pathways which are associated with certain anatomical traits as Kranz cells with thick walls, numerous pits and plasmodesmata, differentiated chloroplasts (Brown 1975) and certain stoichiometric ratios between Kranz cells and mesophyll cells (Hattersley 1984),

TABLE 2

Morphological parameters measured in leaves of twelve species of vascular plants in Tebenquiche.

Parámetros morfológicos medidos en hojas de doce especies de plantas vasculares en Tebenquiche.

	Leaf area cm²	Leaf thickness µm	Epidermal thickness µm	Cuticular thickness µm	Palisade parenchyma thickness µm	Spongy parenchyma thickness µm	Stomatal depth µm	Water storing tissue µm	Stomatal density n/mm²
Distichlis spicata	0.9	158.2	17.4	4.1	9.3	0.0	7.7	0.0	–
Lycium humile	0.2	2,700.0	81.0	4.8	356.6	0.0	4.2	1,219.2	183.1
Nitrophila atacamensis	0.3	1,053.6	29.9	7.1	0.0	0.0	0.0	284.5	92.3
Festuca deserticola	5.2	425.5	12.6	4.1	65.5	0.0	9.5	0.0	–
Puccinellia frigida	0.5	233.3	15.4	4.7	59.5	0.0	14.1	0.0	–
Triglochin palustris	2.2	720.0	42.8	5.9	331.6	0.0	0.0	293.4	116.7
Scirpus olneyi	0	0	22.9	5.1	93.9	0.0	5.6	0.0	–
Scirpus sp.	0	0	25.5	3.7	122.9	0.0	6.6	0.0	167.1
Sarcocornia fruticosa	0	1,373.1	63.3	7.7	276.2	0.0	39.9	871.2	72.0
Juncus balticus	0	0	17.3	8.0	112.1	0.0	0.0	0.0	371.6
Baccharis juncea	1.1	605.4	38.0	4.9	333.3	0.0	11.6	34.6	106.2
Phragmites australis	9.3	277.5	21.0	5.9	57.2	0.0	7.0	0.0	–

* *Juncus balticus, Scirpus olneyi* and *Scirpus* sp. are aphyllous species; thus, leaf thickness could not be measured. All 0 values correspond to parameters that were not present in the sample. The dash corresponds to characters which proved to be impossible of being accurately measured.

TABLE 3

Morphological traits appearing in leaves of twelve species of vascular plants in Tebenquiche. (+ = presence; – = absence).

Caracteres morfológicos presentes en las hojas de doce especies de plantas vasculares en Tebenquiche. (+ = presencia; – = ausencia).

	Unifacial leaf	Crystals	Glands	Vertical leaves	Kranz Anatomy	Folded leaves	Trichomes	Striated cuticle	Sclerenchyma
Distichlis spicata	–	–	+	+	+	+	+	+	+
Lycium humile	+	+	+	+	–	–	–	+	–
Nitrophila atacamensis	+	+	–	+	–	–	–	+	–
Festuca deserticola	–	–	–	+	–	+	+	–	+
Puccinellia frigida	–	–	–	+	–	+	–	+	+
Triglochin palustris	+	+	–	+	–	–	–	+	+
Scirpus olneyi	+	–	–	+	–	–	–	+	+
Scirpus sp.	+	–	–	+	–	–	–	+	+
Sarcocornia fruticosa	+	+	–	+	–	–	–	+	+
Juncus balticus	+	–	–	+	–	–	–	–	+
Baccharis juncea	+	+	–	+	–	–	–	+	–
Phragmites australis	–	–	–	+	–	–	–	+	+

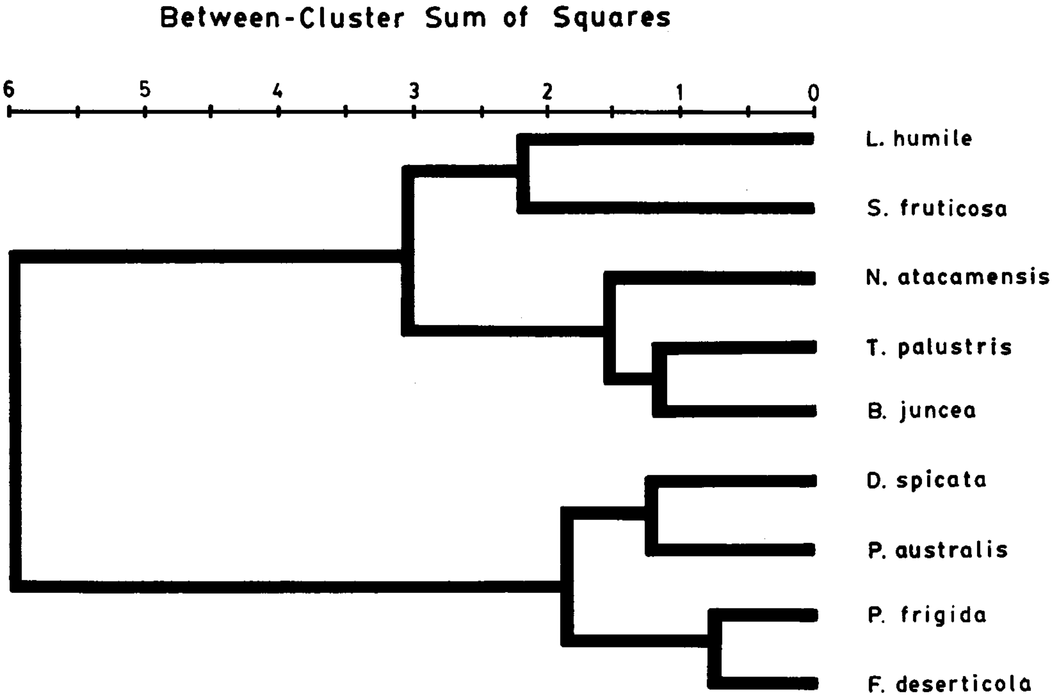


Fig. 3: Similarity dendrogram showing morphological affinities among the analyzed leaves based on Ward's Minimum Variance Cluster Analysis.

Dendrograma de similitud que muestra las afinidades morfológicas entre las hojas analizadas, basado en Ward's Minimum Variance Cluster Analysis.

TABLE 4

Parameters producing physical stress and leaf anatomical traits linked to them.

Parámetros que producen tensiones físicas y rasgos anatómicos foliares asociados a ellos.

Parameters producing physical stress	Biological problems originated in leaves	Anatomical trait that handles biological problem
Drought	High evapotranspiration	Small leaf size (low external and internal surface/volume rates) Kranz Anatomy Protected stomates
High solar radiation	Over heating	Water storing tissues Small leaf size
	Physical damage	Thick cuticles Waxes Vertical position of photosynthetic tissues
Wind	Mechanical damage	Low size individuals Small leaf size Rounded shapes Sclerenchyma Lack of trichomes
High salt concentration	Non-favorable water potential	Salts glands
	Toxicity	Crystals Silica cells

occur in *Distichlis spicata* (Fig. 4b). This has been reported for the same species by Hansen *et al.* (1976). The presence of Kranz anatomy and C_4 photosynthesis seems to be a mechanism for overcoming photosynthesis impairment due to lowered CO_2 concentrations, which occurs in response to water conservation mechanisms.

All species, except *Juncus balticus* showed stomatal protecting structures such as sunken stomata (Fig. 4c), prominent outer edges in guard cells cuticle, wax rods which nearly hide guard cells (Fig. 4d), cuticle striations and papilose cells (Fig. 4e). Trichomes form a thick net protecting stomata in *Festuca deserticola*, within a nearly closed chamber encircled by folded leaves (Fig. 4f); ridges and furrows on the adaxial surface of some species offer a secure location for stomata within the furrows (Fig. 4e). All these devices offer protection against water loss as vapor from the stomatal cavity to the atmosphere by diminishing the water vapor pressure difference between mesophyll and stomata surrounding environment.

In an area with 42 mm annual rain (Di Castri & Hajek 1976) with an extremely saline lake whose water is apparently unavailable for plants, water storing should be a problem. Thus, water has to be conveniently stored and this is accomplished by thin walled colorless parenchyma in many of the species (Fig. 4a), with the outstanding role of tracheoid idioblasts in *Sarcocornia fruticosa* (Fig. 5a). These structures had been reported by Fahn and Arzee (1959) and they seem to hold water by hydrogen bonding to their cell walls (Mauseth 1988). Sclerenchyma cells which appear as longitudinal strands (Fig. 5b), surrounding vascular bundles or as a hypodermis (Fig. 4f) could accomplish water storing functions in the same fashion as tracheoid idioblasts. All plants devoid of water storing parenchyma had sclerenchyma, supporting the above mentioned assumption.

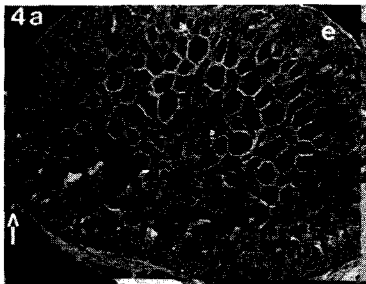


Fig. 4a: Transverse SEM section through a *Lycium humile* leaf showing double layered epidermis, palisade parenchyma, water storing parenchyma, vascular bundle, glandular trichomes and a compact leaf with no air spaces, 45 x (e: double layered epidermis, arrow: glandular trichomes).

Corte transversal en MEB por una hoja de *Lycium humile* mostrando epidermis con dos capas, parénquima en empalizada, parénquima reservante de agua, haz vascular, tricomas glandulares y una hoja compacta sin espacios aeríferos, 45 x (e: epidermis con dos capas, flecha: tricomas glandulares).

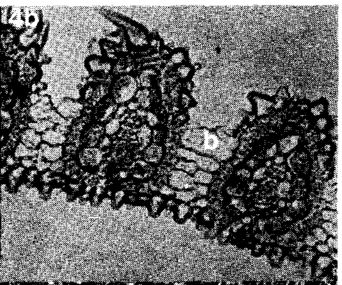


Fig. 4b: Transverse section through a *Distichlis spicata* leaf showing papilose epidermis with salt gland, bulliform cells, ridges and furrows on the abaxial surface and Kranz anatomy, 300 x (b: Bulliform cells, arrow: salt gland).

Corte transversal por una hoja de *Distichlis spicata* mostrando epidermis papilosa, con una glándula de sal, células buliformes, costillas y depresiones en la cara abaxial y anatomía de Kranz, 300 x (b: células buliformes, flecha: glándula de sal.).

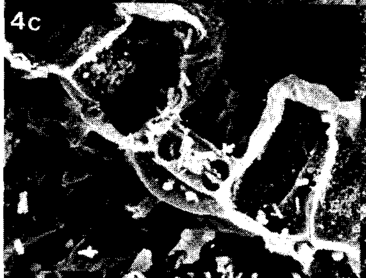


Fig. 4c: Transverse SEM section through a *Sarcocornia fruticosa* stem showing epidermal cells and a sunken stomate loaded with salt crystals, 1,000 x.

Corte transversal en MEB por un tallo de *Sarcocornia fruticosa* mostrando estomas y epidermis cubierta con escamas de cera, 1.000 x (s. estomas).

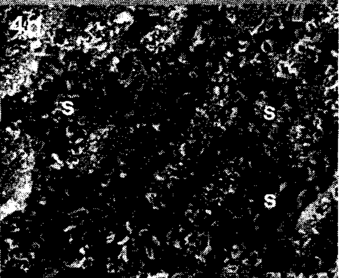


Fig. 4d: Abaxial epidermal SEM view of a *Puccinellia frigida* leaf showing stomate and epidermis covered with wax rods, 1.000 x (s: stomate).

Vista en MEB de la superficie abaxial de una hoja de *Puccinellia frigida*, mostrando estomas y la epidermis cubierta con bastones de cera, 1.000 x (s: estoma).

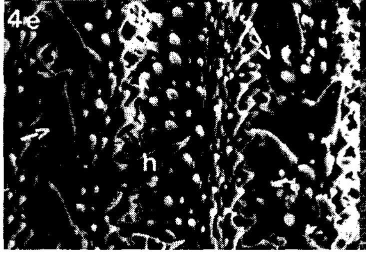


Fig. 4e: SEM view of the adaxial surface of a *Distichlis spicata* leaf showing papilose epidermal cells, hairs and stomatal location within the furrows, 300 x (h: hair, arrow: stomate).

Vista en MEB de la superficie odaxial de *Distichlis spicata* mostrando epidermis papilosa, pelos y estomas localizados en las depresiones, 300 x (h: pelo, flecha, estoma).

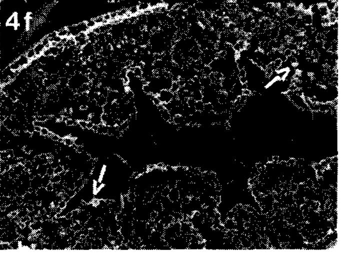
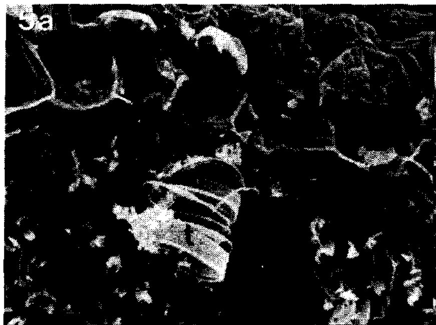
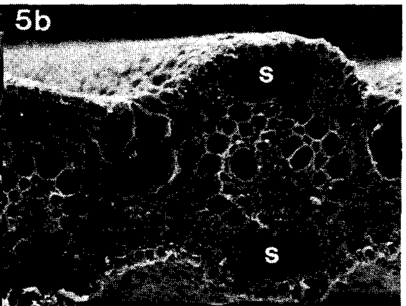
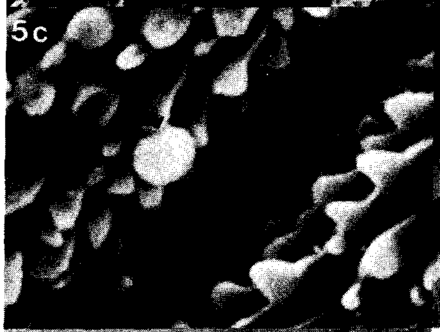


Fig. 4f: Transverse SEM section through a *Festuca deserticola* leaf showing folded leaf, trichomes covering the adaxial epidermis, stomates located within the furrows on the adaxial epidermis and a lignified hypodermis, 150 x (h: hypodermis, arrow: stomate).

Corte transversal en MEB por una hoja de *Festuca deserticola* mostrando lámina plegada, tricomas cubriendo la superficie adaxial, estomas en las depresiones de la epidermis adaxial e hipodermis lignificada, 150 x (h: hipodermis, flecha: estoma).







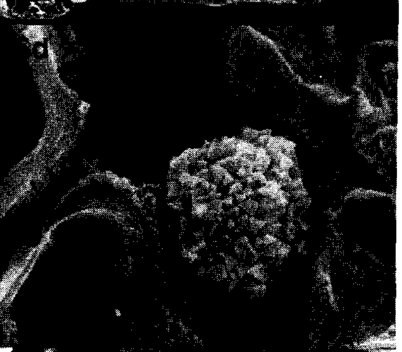


Fig. 5a: Transverse SEM section through a *Sarcocornia fruticosa* stem showing water holding tracheoid idioblasts within palisade parenchyma, 450 x (t: tracheoid idioblast).

Corte transversal en MEB por un tallo de *Sarcocornia fruticosa* mostrando idioblastos traqueidiformes retentores de agua en el parénquima en empalizada, 450 x (t: idioblastos traqueidiformes).

Fig. 5b: Transverse SEM view of a *Phragmites australis* leaf showing sclerenchyma bundles which cover the area between the vascular bundles and the upper and lower epidermis, 200 x (s: sclerenchyma).

Corte transversal en MEB por una hoja de *Phragmites australis* mostrando bandas de esclerénquima que cubren el área entre los haces vasculares y la epidermis superior e inferior, 200 x (s: esclerénquima).

Fig. 5c: SEM view of the adaxial epidermis on a *Distichlis spicata* leaf showing salt glands, 1.000 x (arrow: salt gland).

Vista en MEB de la superficie adaxial de *Distichlis spicata* mostrando glándulas de sal, 1.000 x (flecha: glándula de sal).

Fig. 5d: Transverse SEM section through a *Lycium humile* leaf showing a cluster of crystal sand in a Parenchymatic cell, 2.000 x (c: crystal sand).

Corte transversal en MEB por una hoja de *Lycium humile* mostrando un conglomerado de cristales arenosos en una célula parenquimática, 2.000 x (c: cristales arenosos).

Fig. 5e: Transverse section through a *Baccharis juncea* leaf showing an aggregate crystal complex of styloid crystals in a stomatal chamber, 400 x (arrow: crystal complex).

Corte transversal por una hoja de *Baccharis juncea* mostrando un conjunto agregado de cristales estiloideos en la cámara estomática, 400 x (flecha: conjunto de cristales).

Fig. 5f: Transverse SEM section through a *Nitrophila atacamensis* leaf showing a cluster of styloid crystals in a parenchyma cell, 1.500 x (arrow: crystal cluster).

Corte transversal en MEB por una hoja de *Nitrophila atacamensis* mostrando un conglomerado de cristales estiloideos en una célula parenquimática, 1.500 x (flecha: conglomerado de cristales).

Atacama has one of the clearest atmospheres in the world. This means that solar radiation is very intense and plants living in the area must endure it all year around. Visible radiation is necessary for photosynthesis but both extremes of the solar spectrum may cause damage in the structure and physiology of leaves. Near infrared radiation can produce extremely high leaf temperatures and ultraviolet radiation may cause a break down of nucleic acids and proteins (Mulroy 1979). Plants use several strategies to avoid excess of solar radiation such as changing leaf angle, small leaf size, glaucescence, pigments and pubescence. All plants had a vertical leaf orientation and this seems to be an adaptive trait responding to permanent high solar radiation intensities. This is especially true for the Chenopodiaceae, Compositae, Juncaginaceae and Solanaceae, and could be considered as a morphological family trait in Gramineae and Cyperaceae. Leaf angle which may reduce the amount of incident radiation upon the leaf surface has been reported to be a significative strategy in plants living in mediterranean type ecosystems (Montenegro & Riveros de la Puente 1977, Ehleringer & Comstock 1985). These plants change their leaf angle in response to solar radiation intensities, which also change according to daily and seasonal patterns in their habitat. Thus, permanent vertical leaf orientation should be a response of plants to permanent high radiation in desert habitat. Salt containing glandular trichomes are also a means of reducing leaf absorptance (Black 1954, Mooney *et al.*, 1977) along with thick cuticles with occur in all species. Cuticular modifications as striations and wax depositions could be considered as complementary devices for avoiding harmful solar radiation.

Trichomes have been described in protecting leaves from sunlight (Johnson 1975, Alberdi & Oyarce 1976) and excess evapotranspiration (Montenegro *et al.*, 1980, Montenegro 1984). Surprisingly these structures appear in only two species; *Distichlis spicata* and *Festuca deserticola* (Fig. 4e and Fig. 4f); this absence could be a response to wind which is strong in the area and carries abrasive sand and salt particles. An indumentum could be damaged and would end up loaded with heavy useless particles which could seriously harm plant structure. Strong wind could account for the small plant leaf size, which has already been mentioned.

High salt concentration in soil and water produces very low water potentials that cause difficulties in water uptake by the roots. This probably initiates the development of lower water potentials within the plant which, coupled with high salt concentrations, could be stressful to biological activity and need to be carefully controlled. An interesting way to do this is by developing salt excreting glands that pump ions out of the plant. These have been studied in many plants (Mozafar & Goodin 1970, Hansen *et al.*, 1976) and described as modified pluricellular trichomes located on the leaf epidermis (Fig. 5c). Other salt controlling methods have been described and actually observed in our study. The most obvious one is crystal formation (Franceschi & Horner 1980) which occurred in many of the species (Figs. 5d, 5e, 5f). Crystals are considered as osmoregulation devices which also control internal salt concentrations that could produce toxicity. Silica cells which occur in Graminae and Cyperaceae are also involved in salt controlling processes and provide cutting edges or tips which could discourage herbivore grazing (Poblete, personal observation).

The analyzed plants showed several anatomical traits that can be related to environmental parameters. These traits appeared in clustered patterns among the species suggesting two different leaf forms. One form (corresponding to the upper cluster in Fig. 3) seems to be better adapted to its particular habitat because it appears in six species belonging to four different families (Chenopodiaceae, Compositae, Juncaginaceae and Solanaceae) which are taxonomically unrelated. Besides, their leaf pattern is quite different from the typical pattern shown by most of the species belonging to these families which live in other regions of the country (Montenegro 1984). The other form (corresponding to the lower cluster in Fig. 3) is apparently not quite as related to its particular habitat because it occurs in four species of one family (Gramineae) and most of its anatomical traits do appear in most of the species of the family which live in other parts of Chile.

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