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Leaf anatomy of plants from coastal Mediterranean salt-marshes. Monocotyledons

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ABSTRACT

MATEU ANDRES, I. (1991). Leaf anatomy of plants from coastal mediterranean salt-marshes. Monocotyledons. *Candollea* 46: 345-358. In English, English and Spanish abstracts.

The leaf anatomy of twelve monocotyledon taxa of the mediterranean salt marshes have been studied with particular attention to the mechanisms of adaptation wich allow them to survive in saline conditions. These are compared to the dicotyledons which are studied in an earlier work (MATEU, 1989). The monocotyledons have similar adaptative mechanisms and these are less variable than those of the dicotyledons. They are: several layers of clorenchymatous cells, a reduced number of stomata, thick external cellular walls in the epidermis, abundant mechanical tissue. The first and second of these occur in both the monocotyledons and the dicotyledons, but in the monocotyledons studied water reservant tissue does not occur, and protective trichomes and salt excreting glands are scarce. Also, two of the species have Kranz structure which, together with *Atriplex halimus,* represents ten per cent of all the taxa studied.

RESUMEN

MATEU ANDRES, I. (1991). Anatomía foliar en plantas de saladares mediterráneos costeros. Monocotiledóneas. *Candollea* 46: 345-358. En inglés, resúmenes inglés y español.

Se estudian diversos aspectos anatómicos en las hojas de doce táxones de monocotiledóneas de saladares mediterráneos costeros, Se analizan los mecanismos de adaptación al medio que presentan, y se comparan con los de dicotiledóneas estudiadas en un rabajo anterior (MATEU, 1989). De todo ello, se deduce que las adaptaciones de que se proveen las monocotiledóneas son muy similares en las especies estudiadas, presentando una menor variedad de ellas que las dicotiledóneas. Las adaptaciones que permiten a estas plantas vivir en medios salinos son los clorénquimas con varias capas de células, la escasez de estomas, las paredes celulares epidérmicas externas engrosadas y la abundancia de tejidos mecánicos. De ellas, las dos primeras son comúnes con dicotiledóneas, mientras que carecen de tejidos reservantes de agua y los tricomas protectores o glandulares son escasos. Así mismo, dos de las especies estudiadas presentan anatomía Kranz, lo que junto a *Atriplex halimus* supone un diez por ciento de las plantas estudiadas.

Introduction

This work forms a part of a study on the leaf anatomy of plants found in the coastal salt-marshes of Valencia (Spain). An earlier work (MATEU, 1989) studied the dicotyledons. The ontogenetic differences between the dicotyledons and monocotyledons (HICKEY & WOLFE, 1975; STEEVES & SUSEX, 1988; NELSON & LANGDALE, 1989) together with the differing elasticity of the cellular walls, point to ecophysiological differences between the two groups. On this basis the anatomy of the two groups has been dealt with separately.

DAVIS (1987) has looked at the variability of anatomical characteristics by means of a study of *Puccinellia* reaching the conclusion that these show less plasticity than morphological characteristics, for example, as can be seen from varying size of cells in individual plants subjected to

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different levels of stress. This work, together with the data presented in the earlier work (MATEU, 1989) suggests that the leaf anatomy of different species represents individual adaptations, in the same way as do the genetics of plants adapted to survive particular environments.

Therefore the leaf anatomy of several monocotyledons have been examined with particular attention to their mechanisms of adaptation, analysing and comparing them one with another, as well as with the dicotyledons. Twelve taxa have been studied out of about thirty which are to be found in these salt-marshes. They have been selected randomly with the result that among them are plants with differing degrees of tolerance to and apetite for salt, so that their adaptations may be compared in the same way as were the dicotyledons.

Materials and methods

The collection of samples was made in the same area and by the same means as in the previous work (MATEU, 1989). The anatomical study used fresh materials and followed the methods and techniques indicated therein. The test material has been preserved in the plant collection of the Vegetal Biology Department (VAB) of the University of Valencia (Spain).

The taxa studied are given according to Flora Europaea (TUTIN & al., 1977) and are the following:

Juncus maritimus Lam. ..... *Juncaceae*
Juncus acutus L. subsp. *acutus* ..... *Juncaceae*
Juncus capitatus Weigel ..... *Juncaceae*
Puccinellia festuciformis (Host.) Parl. subsp. *convoluta* (Hornem.) Hughes ... *Gramineae*
Parapholis filiformis (Roth.) Hubbard ..... *Gramineae*
Phragmites australis (Cav.) Trin. ex Steudel ..... *Gramineae*
Aeluropus littoralis (Gouan) Parl. ..... *Gramineae*
Spartina versicolor Fabre ..... *Gramineae*
Scirpus maritimus L. subsp. *maritimus* ..... *Cyperaceae*
Scirpus holoschoenus L. ..... *Cyperaceae*
Schoenus nigricans L. ..... *Cyperaceae*
Carex extensa Good ..... *Cyperaceae*

The data are summarised in Table 2 with the exceptions of the number of stomata wich is given in Table 1. Of all the anatomical characteristics observed, those considered as adaptative are given in Table 3. In this Table, in obtaining the total number of adaptations, a + is given a value of 1. In the case of the cuticle and the external cellular walls of the epidermis, they have been given varying values as adaptations, depending on thickness; G representing a value of 2, M a value of 1 and D a value of 0. By comparison with de dicotyledons, the distribution of chlorenchyma in the monocotyledons examined here can be counted as an adaptation and in every case is given the value of 1.

	Upper	*Lower*
Juncus maritimus	128*	
Juncus acutus	165*	
Puccinellia festuciformis	0	110
Phragmites australis	324	300
Scirpus maritimus	84	90
Scirpus holoschoenus	0	110
Schoenus nigricans	0	140
Carex extensa	0	113

Table 1. — Number of stomata/mm^2.
* express that there are no different upper and lower surfaces.

	Leaves thickn.	*Epidermis*						*Mesophyll*		
		Cells.			*Walls*					
		Upper	*Lower*	*Cuticle*	*Ext.*	*Int.*	*Trichomes*	*Undiff. chlor. thickn.*	*P. E. thickn.*	*N° cell layers*
Juncus maritimus	2000	13	13	2	5	2.5	—	—	30-70	3-6
Juncus acutus	2000	18	18	2	5	2.5	—	—	70-150	3-6
Juncus capitatus	350	80	20-30	2	4-7	2	—	90	—	v.
Pucinellia festuciformis	250	12	12	2	4-6	2	PS	50-70	—	v.
Parapholis filiformis	90	23	23	2	3.5-5	2.5	PS	25	—	v.
Phragmites australis	180	18	18	3	3-4	2-3	—	—	50	2-4
Aeluropus littoralis	130	12	12	2	2.5	2	Gl	—	35	2
Spartina versicolor	120-600	22	22	3	5	2	Gl	—	70	2-3
Scirpus maritimus	350	15	20	2	5	1.5	—	300	—	v.
Scirpus holoschoenus	1200	20	20	2-3	5-7	2	—	—	80-120	2-4
Schoenus nigricans	800	28	28	3	7.5	2	—	80	—	v.
Carex extensa	320	70-140	20	2	8-12	2.5	—	150-200	—	v.

Table 2. — Summary of data (dimensions are given in microns).
Trichomes: PS, siliceous hairs; Gl, glands.

	Roll. leav.	*Stomata*			*Epidermis*				*Cl. P.**	*Scl.***	*Chlor. >2 lay.*	*Total adapt.*
		Low N°	*Deeps.*	*Low. surf. only*	*Cells >15 µm*	*Cutic.*	*Ext. wall*	*Glands*				
Juncus maritimus	—	+	+	—	—	D	M	—	P	++	+	7
Juncus acutus	—	+	+	—	+	D	M	—	P	+	+	7
Juncus capitatus	—	.	—	+	+	D	M	—	G	+	+	7
Puccinellia festuciformis	+	+	+	+	—	D	M	—	G	+	+	8
Parapholis filiformis	+	.	+	—	+	D	M	—	G	++	+	9
Phragmites australis	+	—	+	—	—	M	M	—	G	+++	+	10
Aeluropus littoralis	+	.	+	—	—	D	D	+	P.V.	+++	—	8
Spartina versicolor	+	.	+	—	+	M	M	+	P.V.	++	+	11
Scirpus maritimus	—	+	—	—	—	D	M	—	G	+	+	6
Scirpus holoschoenus	—	+	—	+	+	M	M	—	P	++	+	9
Schoenus nigricans	—	+	+	+	+	M	G	—	G	++	+	11
Carex extensa	—	+	+	+	+	D	G	—	G	++	+	10

Table 3. — Adaptations to the salt-marshes saline soils.

Relative upper/lower epidermic cells sizes: >, bigger in the upper surface; <, bigger in the lower surface. Cuticle: D > 2.5 µm, M 3-5 µm. External cellular wall of the epidermic cells: D > 3 µm, M 3-7 µm, G > 7 µm.

* Chlorophyllic parenchyma situation: P, peripheral; P.V., around the vascular bundles (Kranz); G, overall the mesophyll. ** Sclerenchyma: +, present; ++, abundant; +++, very abundant. In all the other columns: ., absence of date; + presence of character; — absence of character.

These plants manifest similar characteristics of adaptation with many adaptations in common and most variations are merely a matter of degree, but the fact that certain of them are distinct exceptions makes the data unsuitable for mathematical analysis. For this reason the cluster analysis used in the earlier work has not been applied.

Results — Anatomical descriptions

Juncus maritimus Pl. (Pl. I, Fig. 1).

Circular or eliptical section of some 1900 μm diameter. A thin epidermis of 13 μm, with cuticle of 2 μm, whose external cellular walls (5 μm) are roughly double the internal walls (2.5 μm), deepset stomata. Radial mesophyll of well structured palisade parenchyma (30-70 μm) with various lines of radially elongated prismatic cells, enclosing spongy parenchyma of more or less isodiametric polyhedrical cells devoid of chlorophyl, which may be lignified and with intercellular spaces. The parenchyma thins out towards the center of the section leaving a central hollow. Vascular bundles are distributed throughout the spongy parenchyma; they are enclosed by a double shell of which the outer layer is parenchymatous and the inner sclerenchymatous; in some vascular bundles the xylem is partially lignified. Abundant sclerenchyma forming triangular bunches of fibres situated next to the epidermis (CUTLER, 1969; FERNANDEZ-CARVAJAL, 1981; FERNANDEZ-CARVAJAL & al., 1989).

Juncus acutus L. subsp. **acutus** (Pl. I, Fig. 2).

Leaf of eliptical or circular section of some 200 μm in diameter. Epidermis of 8 μm. with cuticle of 2 μm and cellular walls of 5 μm externally and 2-2.5 μm internally. Deepset stomata (165/mm^2). Radial mesophyll of palisade parenchyma (30-70 μm) consisting of various rows of rectangular or polyhedrical cells enclosing the spongy parenchyma of polyhedrical isodiametric cells devoid of chlorophyll, which thin out to leave a central hollow. Vascular bundles are enclosed by parenchymatous and sclerophyllous double shell. Both xylem and phloem may be partially lignified.

Juncus capitatus Weigel (Pl. I, Fig. 3).

Leaf of flat-convex section,small size some 300 μm thick. The cells of the epidermis are much bigger on the upper surface than the lower (80 and 2-30 μm, respectively) but with cuticle (2 μm) and cellular walls (4-7 externally and 2 μm internally) equal on both surfaces. Surface stomata. Mesophyll made of more or less round cells with intercellular spaces, although those towards the epidermis become more rectangular and arrange themselves in a more orderly fashion. The vascular bundles have a double shell of parenchyma and sclerenchyma in which the external layer may break towards the upper and lower surfaces (CUTLER, 1969; FERNANDEZ-CARVAJAL, 1982; FERNANDEZ-CARVAJAL & al., 1989); xylem and phloem lightly lignified.

Puccinellia festuciformis (Host.) Prl. subsp. **convoluta** (Hormen) Hughes (Pl. I, Fig. 4).

Flat even section in the shape of a V (METCALFE, 1960), 250 μm thick. Thin epidermis (12 μm) with cuticle of 2 μm and cellular walls of 4-6 μm externally and 2 μm internally. The upper surface is gently ridged by veins and depressions, the lower surface is smooth. The upper epidermis has bulliform cells in the depressions. There are papillae on both the upper and lower surfaces; Deepset stomata. Undifferentiated chlorophyllic parenchyma (50-70 μm) of more or less round cells which are irregular in size. The position of the vascular bundles correspond to the veins and are sorrounded by a double shell of parenchyma and sclerenchyma. Next to the epidermis and corresponding to the vascular bundles both on the upper and lower surfaces there are small bundles of sclerophyllous fibres like those found on the margins.

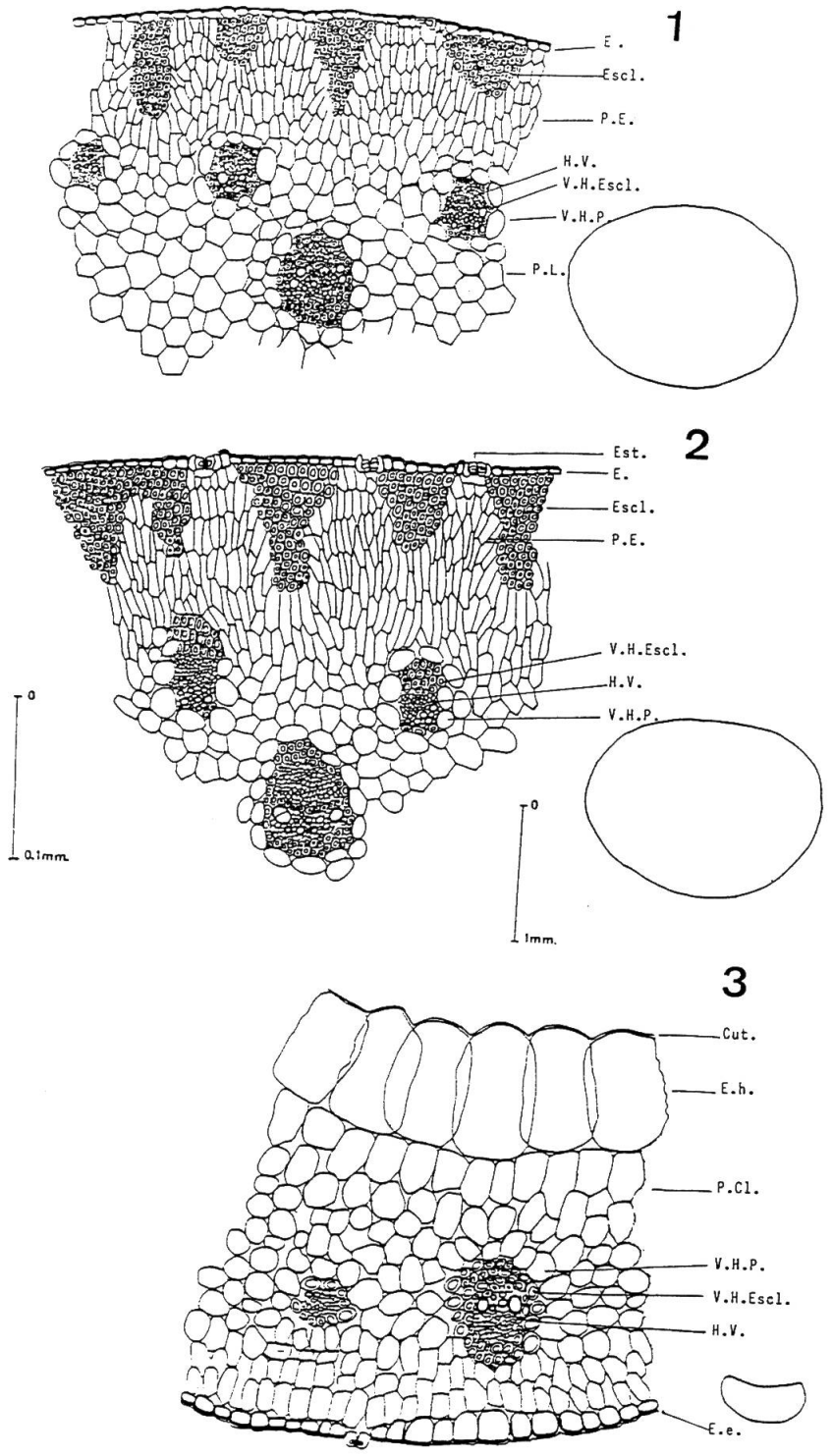
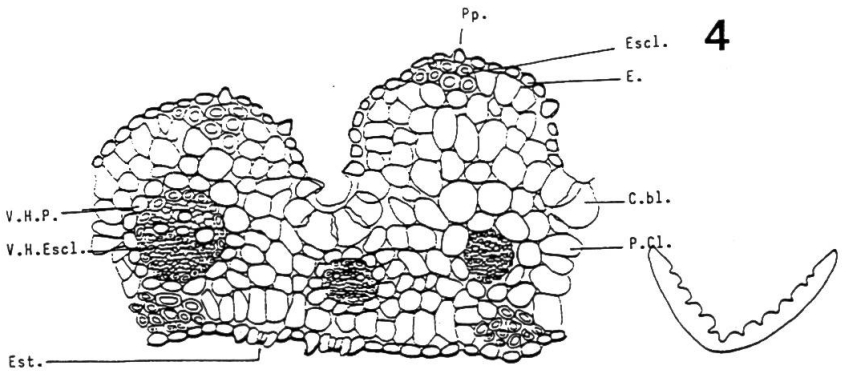


Plate I. — Internal structure and section scheme of the studied taxa.
1, *Juncus maritimus;* **2,** *J. acutus;* **3,** *J. capitatus;* **4,** *Puccinellia festuciformis;* **5,** *Parapholis filiformis;* **6,** *Phragmites australis;* **7,** *Aeluropus littoralis.*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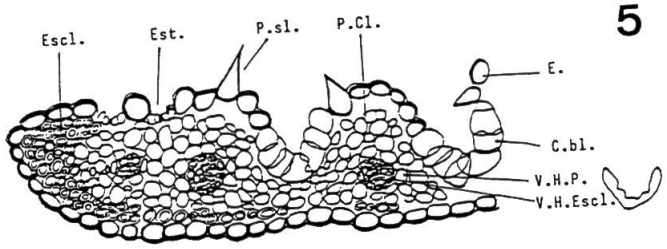
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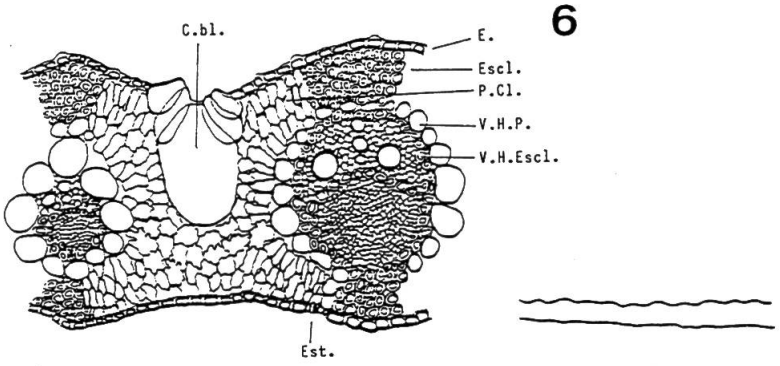
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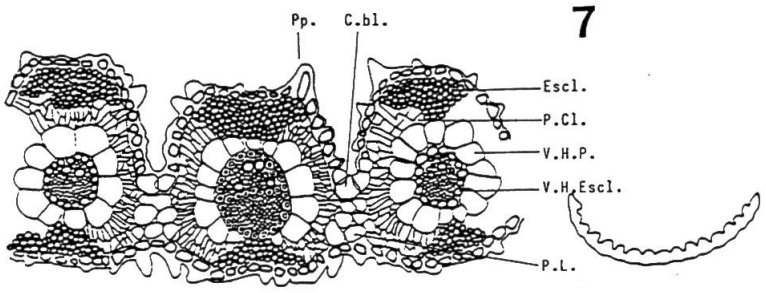
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V.H.P.
V.H.Escl.
P.L.

7

Parapholis filiformis (Roth.) Hubbard (Pl. I, Fig. 5).

Flat even leaf section of 90 μm in the shape of a V, smooth on the lower surface and gently ridged on the upper. The lower epidermis (23 μm) is of lightly lignified, homogeneous cells; the upper epidermis is made up of mostly bulliform cells (VIGNAL, 1979) and in less abundance, cells similar to those of the lower surface; the cuticle is of 2 μm on both surfaces and the external cellular walls of 3.5-5 μm while the internal are 2.5 μm. Short siliceous hairs on the upper surface. Deepset stomata. Mesophyllic parenchyma, which although similar to the spongy type, are homogeneous throughout the section. Vascular bundles correspond to the veins on the upper surface and are enclosed by a double shell of parenchyma and sclerenchyma. Next to the epidermis and all over the leaf there is an almost continuous layer of sclerenchyma, more abundant at the margins and interrupted on the upper surface by the bulliform cells.

Phragmites australis (Cav.) Trin ex Steudel (Pl. I, Fig. 6).

Smooth section of 180 μm thickness, with slight undulations more marked on the upper surface than the lower. Epidermis lightly lignified, (18 μm) with cuticle of 3 μm and external cellular walls (3-4 μm) slightly thicker than the internal walls (2-3 μm). In depressions there are groups of fine bulliform cells, the central cell being much larger than the others and penetrating the mesophyll more than half way into the section (METCALFE, 1960). Papillae reduced in size. Deepset stomata (300-324/mm^2), whose frecuency is the highest of the taxa studied. Undifferentiated mesophyll equal on both surfaces, with chlorophyllic parenchyma (50 μm) of 2-4 layers of irregular cells, in which adjacent cells interlock, situated around the vascular bundles. The vascular bundles are of two distinct sizes. All are enclosed by a double shell, the external parenchymatous layer is well formed in the case of the small bundles, while in the large bundles the cells diminish in size towards the upper and lower surfaces and may dissapear altogether in which case the internal sclerenchymatic layer becomes one with the bundles of sclerenchyma situated between the vascular bundles and the epidermis.

Aeluropus littoralis (Gouan) Parl. (Pl. I, Fig. 7).

Leaf of some 130 μm thick, an even and smooth section with undulations on both surfaces although greater on the upper than the lower. Heavily lignified epidermis of 12 μm with cuticle of 2 μm and internal and external cellular walls aproximately equal (2.5 and 2 μm). Abundant papillae on both surfaces. Sparse glands and deepset stomata. Equal mesophyll on both surfaces consisting of two rows of small cells, rectangular or prismatic, distributed radially around the vascular bundles, corresponding to the Kranz structure (SHOMER-ILAN & WAISEL, 1973, 1976; DOWNTON & TÖROKFALVY, 1976) and a small parenchyma which may be considered to be of the spongy type corresponding to the canals. Vascular bundles of two types accordingly to size (METCALFE, 1960). The shell is double in the case of the small bundles and well structured whereas in the larger bundles the parenchymatous layer may disappear so that the sclerophyllous layer comes into contact with the sclerophyllous fibres which occur both above and below, between the shell of the vascular bundle and the epidermis.

Spartina versicolor Fabre (Pl. II, Fig. 1).

Smooth even section subject to some degree of rolling inwards onto its upper surface, with ribs of considerable size on the upper surface, bigger ribs alternating with smaller. Because of this the thickness of the leaf varies between 120 and 600 μm. Lignified epidermis particularly on the upper surface with cells of 22 μm, cuticle of 3 μm with external walls thicker than the internal walls (5 and 2 μm respectively). Abundant papillae on the upper surface. Few glands distributed on both surfaces (METCALFE, 1960; ANDERSON, 1974). Deepset stomata. Equal mesophyll on both surfaces, with chlorophyllic parenchyma (70 μm) at one or two layers of cells grouped around the vascular bundles, typical of the Kranz structure (LONG, 1983). On the upper surface of the larger veins there is a basic parenchyma of large, prismatic cells which does not occur on the smaller veins. Vascular bundles of two types, according to size and corresponding to ribs; the larger have partially

lignified xylem. Vascular bundles have a double shell of parenchyma and sclerenchyma extended towards the upper and lower surfaces so that they take on a triangular shape (METCALFE, 1960; REINHOLD & QUEEN, 1974). Between the vascular bundles and the lower epidermis there are small bundles of sclerophyllous fibres which also occur on the upper surface at the ridge of the larger veins.

Scirpus maritimus L. subsp. **maritimus** (Pl. II, Fig. 2).

Flat even section of 350 μm thickness in the characteristic shape of an open V. Epidermis (15-20 μm) with cuticle of 2 μm and cellular walls thicker externally (5 μm) than internally (2.5 μm). Surface stomata, aproximately equal in frequency on both surfaces (84/mm^2 on the upper surface and 90/mm^2 on the lower). Equal mesophyll on both surfaces with chlorophyllic parenchyma (300 μm) with rectangular cells in the center of the mesophyll. Vascular bundles are enclosed by a double shell, the internal layer is schlerophyllous and the external, which is enlarged towards the upper surface, is parenchymatous. There are bundles of sclerophyllous fibres, like those on the margins, situated between the vascular bundles and the epidermis both above and below.

Scirpus holoschoenus L. (Pl. II, Fig. 3).

Leaf of flat-convex section 1200 μm thick. Epidermis (20 μm) with cuticle of 2-3 μm and external cellular walls (5-7 μm) thicker than the internal walls (2 μm). Surface stomata (110/mm^2.) absent on the upper surface. Mesophyll consisting of chlorophyllic palisade parenchyma (80-120 μm) of 3-4 layers of cells enclosing spongy parenchyma of large rounded cells, devoid of chlorophyll and with large intercellular spaces which break off leaving a central hollow. Vascular bundles alternate in size; all of them have a double shell of which the parenchymatous outer layer breaks off towards the upper and lower surfaces and the internal sclerophyllous layer joins with the xylem, which is partially lignified, at the base of the bundle. In the upper part there are bundles of sclerophyllous fibres which can be joined to other triangular fibres reaching away from the epidermis towards the center of the section. Between each pair of vascular bundles and on the edges of the two parenchyms there are air channels.

Schoenus nigricans L. (Pl. II, Fig. 4).

Flat-convex section 800 μm thick. Epidermis (28 μm) with cuticle of 3 μm and external cellular walls (7-8 μm) thicker than the inner walls (3 μm). Deepset stomata (150/mm^2) absent on the upper surface. Undifferentiated mesophyll (80 μm) of rectangular or circular cells, with frequent intercellular spaces, which break off in the center leaving a hollow. Vascular bundles have a double shell of unevenly structured parenchyma externally and sclerenchyma internally. Xylem mostly lignified. There are air channels between some vascular bundles. Next to the epidermis there are flat bundles of sclerophyllous fibres.

Carex extensa Good. (Pl. II, Fig. 5).

Leaf of flat even section of 320 μm thickness. The epidermis differs between the upper and lower surfaces. On the lower surface the cells are of equal size (20 μm) while on the upper they are much larger and varying in size between 70 and 140 μm. The cuticle is of 2 μm, and the external cellular walls are thick (8-12 μm) whereas the internal walls are not (2.5 μm). The upper surface is devoid of stomata but there are deepset stomata on the lower surface with an average frequency of 113/mm^2. Equal mesophyll on both surfaces with chlorenchyma similar to the spongy type which is continuous from the upper surface to the lower (150-200 μm). There are vascular bundles of two types, some are enclosed by a double shell of parenchyma and sclerenchyma, others are enclosed by a column of sclerenchyma which stretches between the two surfaces of the leaf. Also numerous irregularly spaced air channels.

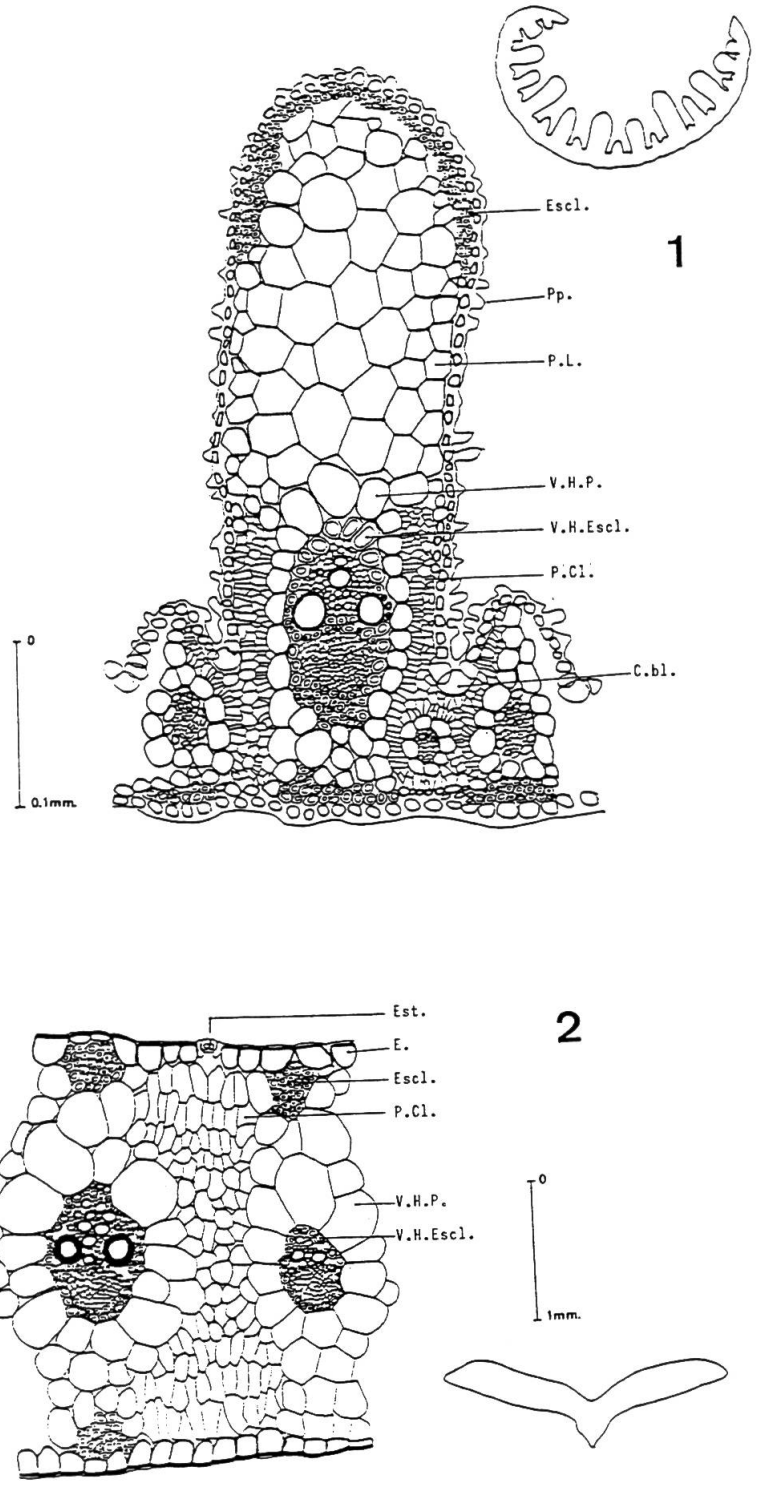
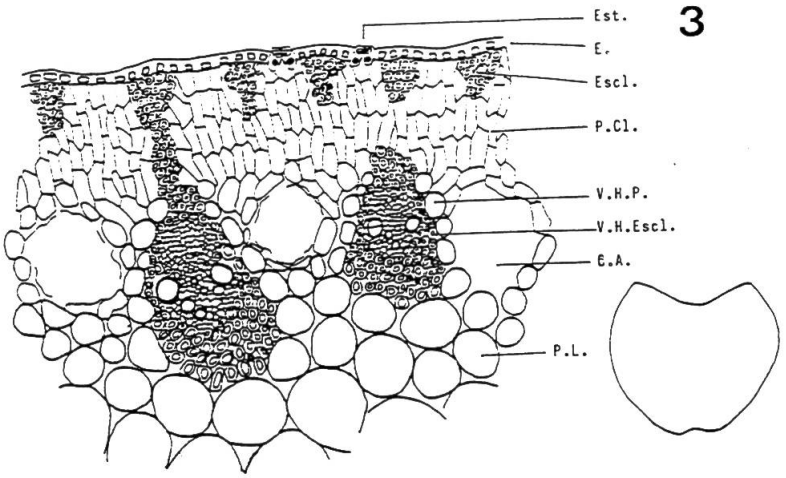


Plate II. — Internal structure and section scheme of the studied taxa.
1, *Spartina versicolor;* **2,** *Scirpus maritimus;* **3,** *S. holoschoenus;* **4,** *Schoenus nigricans;* **5,** *Carex extensa.*
The scales are: 0.1 mm for the anatomical drawings; 1 mm for the sections schemes.
The abbreviations used are: C. A. aeriferous channel; C. bl. bulliform cells; Cut. cuticle; E. epidermis; E. e. lower surface epidermis; E. h. upper surface epidermis; Escl. sclerenchyma; Est. stomata; H. V. vascular bundle; P. Cl. undifferentiated chlorophyllic parenchyma; P. E. palysade parenchyma; P. L. spongy parenchyma; P. p. papillae; P. sl. siliceous trichomes; V. H. Escl. sclerenchymatic bundle sheath; V. H. P. parenchymatic bundle sheath.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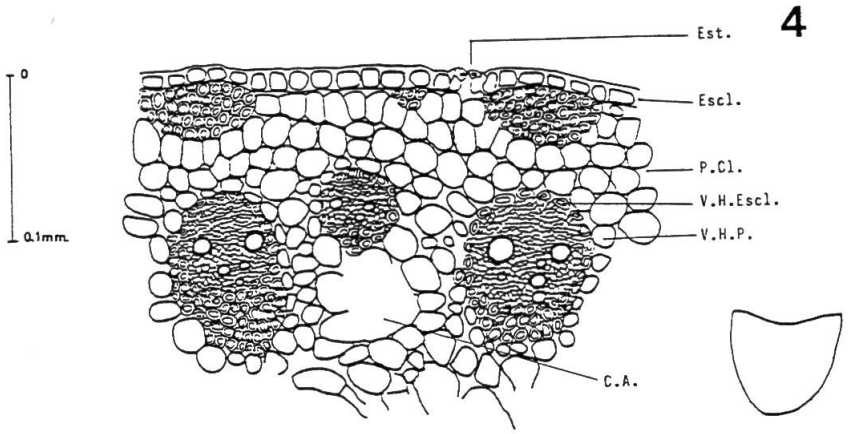
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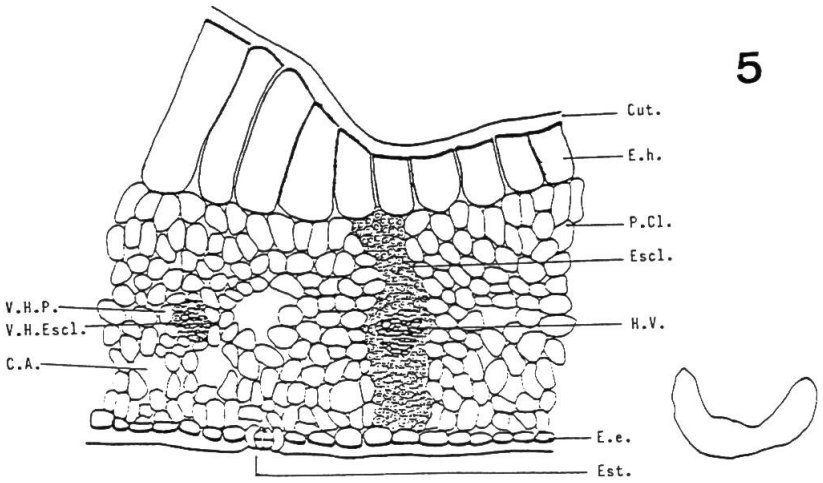
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Results — Synthesis of data

Leaf section

Among the varying shapes and thicknesses of the leaf sections, it is possible to distinguish three groups. The first consists of leaves of circular section (*Juncus maritimus* and *J. acutus*). The second consists of leaves which although almost circular, it is possible to distinguish an upper and a lower surface. The third group consists of plants with thin, flat leaf sections, varying in thickness between 90-350 µm (*Spartina versicolor* varies considerably in thickness according to its ribs and depressions between). Of this last group, five (*Puccinellia festuciformis, Parapholis filiformis, Phragmites australis, Aeluropus littoralis* and *Spartina versicolor*) can curl in on themselves, in towards the upper surface, making a scroll shape.

Epidermis

Only *Puccinelia festuciformis* and *Parapholis filiformis* have small silicic hairs on the upper surface and these are few. The epidermis is monostratified in all cases with relatively large cells varying considerably in size between 12 and 140 µm (KUMMEROW, 1973). They are of equal size on the upper and lower surfaces in nine cases, *Scirpus maritimus* have larger cells on the lower surface than the upper, while *Juncus capitatus* and *Carex extensa* have much bigger cells on the upper surface. In the latter case the cells vary noticeably between 70-140 µm.

The cuticle is similar in all the species (2-3 µm) being of what may be considered average thickness (SHIELDS, 1951; KUMMEROW, 1973; ST. OMER & SCHLESSINGER, 1980). As in the dicotyledons, the lateral cellular walls are thin (up to 2 µm) while the external walls are at least double in thickness than the internal walls, with the single exceptions of *Phragmites australis,* while in *Scirpus maritimus, Schoenus nigricans* and *Carex extensa* they are much bigger externally than internally. There is no difference, in this feature, between the cells of the upper and lower surfaces of the same leaf. Only two species (*Aeluropus littoralis* and *Spartina versicolor*) have salt excreting glands.

The stomata are deepset in nine cases, and on the surfaces in the others; none of them have protective structures. The stomata are not in great abundance although all the plants show more stomata than the dicotyledons. *Phragmites australis* distinguishes itself from the others by its relatively high quantity of stomata (324/mm^2), characteristic of mesophytic plants. Of the eight taxa whose stomata have been counted, four have the same number on the upper and lower surfaces (of these two are of circular section), while in the other four the upper surface is devoid of stomata (of these only *Puccinellia* has the scroll shape).

Mesophyll

Of the leaves examined, *Juncus maritimus* and *J. acutus* have mesophyll of radial symmetry, the others have equal mesophyll on both the upper and lower surfaces. The mesophyll consists of chlorophyllic parenchyma which is always made up of two or more layers of cells, and is of one particular type in each species. The chlorenchyma resembles the palisade type in *Juncus maritimus, J. acutus* and *Scirpus holoschoenus* while in *Puccinellia festuciformis, Parapholis filiformis, Phragmites australis, Scirpus maritimus, S. holoschoenus* and *Schoenus nigricans* it resembles the spongy type. *Aeluropus littoralis* and *Spartina versicolor* have the Kranz structure (SHOMER-ILAN & WAISEL, 1973, 1976; DOWNTON & TÖROKFALVY, 1974; LONG, 1983). Chlorophyllic parenchyma may be the only type of parenchyma, but there may also be undifferentiated parenchyma filling the center of the mesophyll. As already stated in the case of the dicotyledons, the larger number of layers of palisade parenchymatous cells is related to salinity produced by ClNa (POLYAKOFF-MAYBER & GALE, 1975), and entails an increase in the photosynthetic capacity of the leaf and greater facility of water circulation through the mesophyll, particularly in the plants with the Kranz anatomy (KEMP & al., 1983; ROBICHAUX & PEARCY, 1984).

Mechanical tissues

All the taxa studied employ sclerenchymatic fibres as mechanical tissue. Its abundance varies between small bundles of fibres situated below the epidermis and separate strings also situated

below the epidermis forming what appear in the section as columns reaching from the epidermis, as far as the vascular bundles, and which form "girders", according the nomenclature used by DICKINSON (1975), running longitudinally down the whole leaf. Moreover all the plants have a sclerophyllous shell enclosing the vascular bundles.

Discussion

The leaf anatomy of the plants studied show diverse anatomical adaptations to the saline environment which occur with varying frequency; they are summarized in Table 3. To these must be added the average thickness of the cuticle and the thickened cellular external walls of the epidermis which are found to be almost constant. The number of adaptations occurring in each of the taxa studied falls between 6 and 11, which is of numerically small variability. This together with the fact that these adaptations do not vary very much within the group, shows a considerable degree of homogeneity in the monocotyledons.

Of the plants which have distinguishable upper and lower surfaces, five are scrolled, being generally with thin leaves and only those with a circular or flat convex section achieve more than 350 μm thickness. Only *Spartina versicolor* reaches a thickness of 6000 μm in some parts of the section, owing to the development of the ribs on the upper surface.

At the epidermic level, the number of stomata per surface unit is low, with the exception of *Phragmites australis,* and in most cases they are deepset. The cellular size of the epidermic cells, is frequently large, and unlike the dicotyledons, the monocotyledons thicken the external cellular walls of the epidermis but not the cuticle. According to ROZEMA & al. (1987) the rigidity of these thickened cellular walls is important to the maintenance of water content against saline conditions and drought at the same time as helping the mechanical tissues.

The chlorophyllic parenchyma is of a particular type in each case, more or less resembling either the palisade or the spongy type, or of an undifferentiated type in some cases, and always consisting of several cell layers.

Perhaps the most characteristic adaptation of these taxa is the abundance of sclerenchymatic fibres. This tissue protects the plant from damage by drought and is also supported in this function both by thickened epidermal cell walls (WYLIE, 1943) and sclerified parenchymatic tissues.

Two of the taxa studied have the Kranz structure (*Aeluropus littoralis* and *Spartina versicolor*) which together with *Atriplex halimus* suggests a high proportion of plants with this structure (KENNEDY & al., 1980) between those of the salt-marshes; this coincides with data collected by ECHEVARRIA & al. (1988) in the Odiel (Sevilla, Spain).

Conclusions

The leaves of the monocotyledons studied manifest similar characteristics with less variability in the mechanisms of adaptation than the dicotyledons. Also both groups are different in the mechanisms of adaptation which they adopt even though they have some in common.

Of the monocotyledons, the most frequent adaptations are the abundance of supportive tissue, the occurrence of various layers of chlorophyllic parenchyma, the scarcity of stomata frequently deepset and the thickness of the external cellular walls in the epidermis. From this it may be deduced that these are the adaptations which allow them to live in saline environments. To these can be added other adaptations occurring with less frequency such as the scrolling on the upper surfaces, the absence of stomata on the lower surface, and the occurrence of salt-excreting glands.

Among the differences in adaptations separating the monocotyledons from the dicotyledons, should be noted that sclerenchyma is highly developed while aquiferous parenchyma is absent (ROZEMA & al., 1987), the low frequency of salt excreting glands, and the low density of trichomes. On the contrary, the high number of layers making up the chlorophyllic parenchyma, the low frequency of stomata and the thickening of the external cellular walls of the epidermis, are common to both groups of plants.

In this way, we can see that most of the plants growing in the salt-marshes, fall into one of three adaptative syndromes, the principal characteristics of these are the sclerophylly shown by the

monocotyledons, succulence and the salt-eliminating glands shown by the dicotyledons. A number of other, although less frequent adaptations, can be observed in these plants. All of them together with physiological and biochemical mechanisms, permit them to live in this extremely inhospitable environments.

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