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## Vegetative Morphology and Anatomy of the Salt Marsh Rush, *Juncus roemerianus*

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# VEGETATIVE MORPHOLOGY AND ANATOMY OF THE SALT MARSH RUSH, *JUNCUS ROEMERIANUS*

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ABSTRACT    The extensive rhizome development found in *Juncus roemerianus* makes this species unique among rushes and is a biological feature responsible, in part, for its domination of large tracts of salt marsh. Branching in certain mature plants is distinctly sympodial, while in most it is obscured by precocious development of the continuation bud and appears to be monopodial. Each vegetative unit is composed of a scaly rhizome which grows to varying lengths and then abruptly turns up at the end to become an erect shoot. A continuation rhizome consistently arises from an axillary bud in a ventral scale leaf. Transitional leaves (large scale leaves) accompany development of the erect shoot. Rhizome scales, transitional and foliage leaves are distichously arranged and in the same vertical plane. The culm forms through an elongation of an internode of an erect shoot. Other rhizomes may also arise from buds in the axils of the transitional and foliage leaves. From one to seven terete leaves with a bifacial sheath are produced from the apical meristem of the erect stem. Fibrous roots occur laterally on erect shoots. Non-fibrous roots occur on the ventral surface to the rhizomes. The internal rhizome and root anatomy resembles that reported for most other species of *Juncus* while the leaf anatomy is very similar to that of *Juncus maritimus* and *Juncus acutus.*

## INTRODUCTION

*Juncus roemerianus* Scheele is a rush dominating major tracts of salt marsh on the Atlantic and Gulf coasts of the United States (Eleuterius, manuscript in preparation). The most successful herbaceous plants occurring in these maritime marshes are those which are perennial and reproduce vegetatively by vigorous rhizome growth, thus leading to the formation of dense stands. Once established, these species do not generally rely on the sexual cycle for maintenance of the closed stand. The importance of understanding the structure of herbaceous species has become apparent in the study of crop plants where solution of practical problems arises (Hayward 1938; Bonnett 1935, 1940). Only through fundamental knowledge of the pattern of growth, entailing basic morphology and anatomy, can proper analysis of variation in species be attained. Structural studies of salt marsh species have similar importance since successful management of estuaries will ultimately require familiarity with each wild species to the same extent and detail now available for cultivated crop plants.

Although there are several reports (Adamson 1925; Cutler 1969; Stace 1970) on the internal anatomy of various *Juncus* species, comparable studies on the vegetative morphology are lacking. Some general morphological aspects of certain rushes are described by Buchenau (1906) and Richards and Clapham (1941). Anderson (1974) in a general anatomical survey of seven salt marsh plants in North Carolina also included descriptions of some anatomical features of *J. roemerianus.* The present study describes in detail the vegetative morphology, pattern of growth, and anatomy of mature plants of *J. roemerianus* as found in Mississippi.

## METHODS AND MATERIALS

Plant portions consisting of rhizomes (subterranean segments 30 to 60 cm in length) bearing erect shoots and roots were dug out for morphological study. Plant material was taken from more than 20 different habitats. These habitats varied in several ways: leaves of *J. roemerianus* in some places were abundant, sparse, tall, short, in pure stands and associated with other vascular plants. Plants were also examined from low, intermediate and hypersaline marshes, as were plants colonizing new terrain, where they grew without competition. Plant material for anatomical work was fixed in a formalin, proprionic acid and ethyl alcohol solution (FPA), processed using a tertiary butyl alcohol series and embedded in the usual manner. Sections were cut 10–15 microns on a rotary microtome, affixed to slides using Haupt's adhesive and stained with safranin and fast green using standard procedures outlined by Johansen (1940) and Sass (1958).

## VEGETATIVE MORPHOLOGY

### General

A single mature plant of *J. roemerianus* is difficult or impossible to discern by cursory examination in a typical stand. Rhizomes may connect hundreds of erect shoots of a single plant in a relatively small surface area of marsh. The continuous proliferation and subsequent senescence of rhizomes account for the vegetative spread and maintenance of the mature stand (Eleuterius 1975). Long, interconnected rhizomes bearing erect shoots and roots represent a portion of a single clone and serve to illustrate the typical mature plant. The vegetative axes of the mature plant are dimorphic with a clear distinction between horizontal and erect shoots (Figure 1A), but the sequence of events typical of sympodial branching is often obscured by the vigorous growth associated with the horizontal axis.

### The Rhizome

Rhizomes possess tightly overlapping leaf-like scales or

cataphylls which arise ventrally and dorsally. The plane of distichy is vertical. The rhizome apex does not grow indefinitely but eventually becomes an indeterminate erect, leafy shoot. Young rhizome portions are generally larger in diameter than older parts, which become somewhat constricted with age. Rhizomes range in diameter from 2 to 18 mm, the average ones being about 9 mm. The internode length may vary from a millimeter or less to over a centimeter. The rhizome bud is formed periodically in the axil of a scale leaf which arises on the lower surface of the rhizome (Figure 1B—E). The division of the rhizome apex is almost dichotomous with the resulting dorsal meristem being only slightly larger than the ventral. The dorsal and ventral meristems are destined to form the erect shoot and new rhizome, respectively. In most instances the terminal rhizome bud develops precociously and continues to grow at such a rapid rate that the sympodial branching pattern is obscured to the extent that it may be erroneously interpreted as monopodial. The precocious growth of the rhizome bud displaces the terminal bud of the previous unit, which becomes an erect, leafy shoot. This displacement occurs in such a way that the leafy shoot appears to be inserted at the middle or, more often, toward the distal end of the rhizome internode. Occasionally, a rhizome may arise from a bud formed on the dorsal side of the rhizome apex which grows in a direction opposite the terminal rhizome when eviction of the leafy shoot occurs. The apex of the dorsal rhizome becomes oriented in the opposite direction from that arising from the ventral bud. As many as three rhizomes may arise from a single erect shoot. These new rhizomes may occur in the same or opposite directions. Most new rhizomes arise in leaf axils on the side of the erect shoot synonymous to the ventral surface of the rhizome (Figure 1F—G). Deflection of apexes by obstructions in the substratum causes many planes of growth or centrifugal spread of the plant. Consequently, all new rhizome production is in one plane. Axillary buds of the erect shoot, synonymous to the dorsal surface of the rhizome, give rise to new rhizomes which reinvade terrain previously occupied by the plant (Figure 2A and B).

The number of nodes or internodes between erect shoots is variable. In some localities the number may vary from 10 to 18, in others 6 to 12, or 1 to 5. The number varies within the same clone. However, most material examined ranged from 8 to 14 and averaged about 12 nodes between erect shoots. In seedlings only one node may exist between erect shoots (Eleuterius 1975). The distance between erect shoots may be minute to 5.5 centimeters or more, the average being about 2.5 centimeters (Figure 2C—E).

### The Erect Shoot

The mature erect shoot may vary from one to several centimeters in length and consists of a series of nodes and compressed internodes. The growth of the erect shoot is determinate, culminating in the production of terete leaves or a culm. Apparently as the erect shoot develops, the scale leaves become longer and tougher in texture as each successive node is produced. These may be conveniently referred to as transitional leaves, contrasting with the scale leaves of the rhizome and terete foliage leaves. There are generally three to five present on each erect shoot. The arrangement of transitional and foliage leaves is distichous.

A culm is apparently not produced on every erect shoot, some of which then remain leafy throughout their existence. The culm is an elongated internode of the erect shoot, which elevates meristematic tissue destined to be the inflorescence. A red hand circumscribes the floral meristem (node) of the culm and separates the internode region from the bract which subtends the inflorescence. Culm production terminates the life of the erect shoot. However, the rhizome units supporting the erect shoot may remain alive. The culm appears externally much like a leaf; however, it is weakly developed and is broken more easily than the leaf.

### The Foliage Leaf

All foliage leaves are cylindrical or unifacial above the sheath with the abaxial surface to the exterior. The lower portion or sheath of the foliage leaves is bifacial with free margins through which new leaves emerge. All sheaths are rolled and the leaf margins form a slit through which subsequent leaves protrude as they are produced by the apical meristem of the erect shoot. The position of the slit alternates with each successive leaf produced. Leaf production is two-ranked or distichous. Thus, the second leaf generally emerges from a slit on the abaxial surface of the first leaf. As many as seven leaves may arise sequentially from the relatively short erect shoot. The upper portion of terete leaves are stiff and pointed at the end, and may range in diameter from a few millimeters to three-quarters of a centimeter; the average is about 3 millimeters. Mature leaves range in length from 30 to 223 cm, depending on the habitat. Over most of the local population they average about 100 cm.

Figure 1. Vegetative morphology of *Juncus roemerianus*. 1A. A general view of a portion of a mature plant. All units of the sympodium shown are connected and may be traced back to the parental unit on the right. Note that the orientation of most new vegetative units occurs in the same direction with respect to the parental unit (i = inflorescence). 1B. Rhizome apex (a) after forming in this case after five nodes and internodes were produced. 1C. Erect shoot (es) forming by eviction and precocious development of a terminal rhizome bud (rb). The rhizome bud forms in the axil of a scale leaf on the ventral surface of the rhizome. The plane of distichy of the scale leaves is vertical. 1D. Subsequent development of an erect shoot and rhizome buds as shown in preceding view at C. 1E. Later development of erect shoot (es) and rhizome (r). Note development of the two axes are about equal. 1F. General view of rhizomes arising from erect shoots. Note erect shoot (to right) gave rise to two rhizomes. Transitional leaves (t) (scale leaves) accompany early development of erect shoot. 1G. Erect shoot developing after seven nodes and internodes are formed by rhizome apex. Non-branching anchoring roots (nr) arise from nodes on the ventral surface of rhizome.
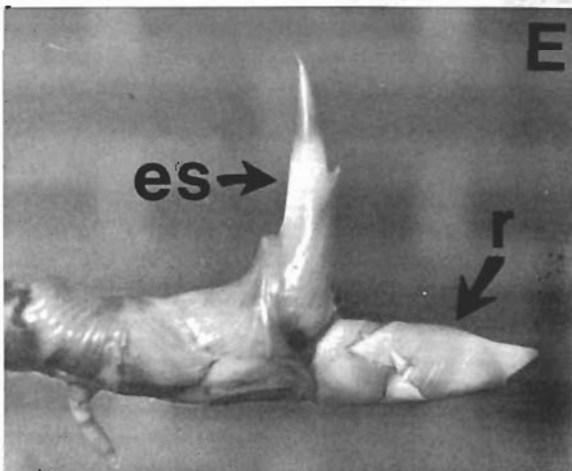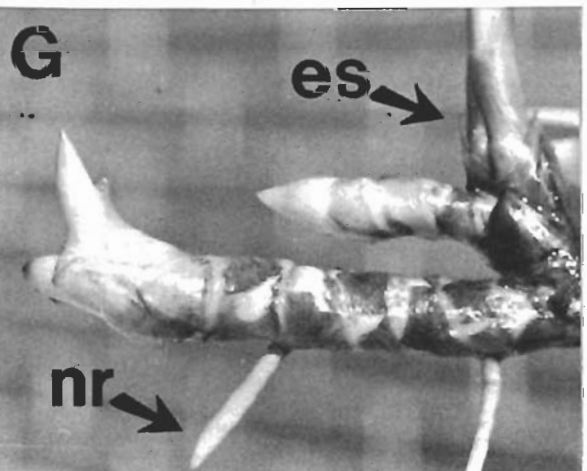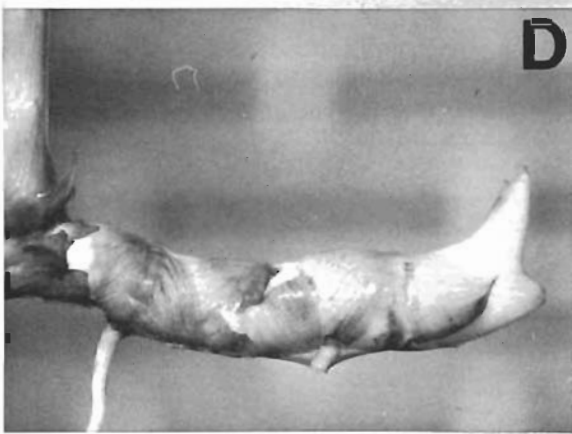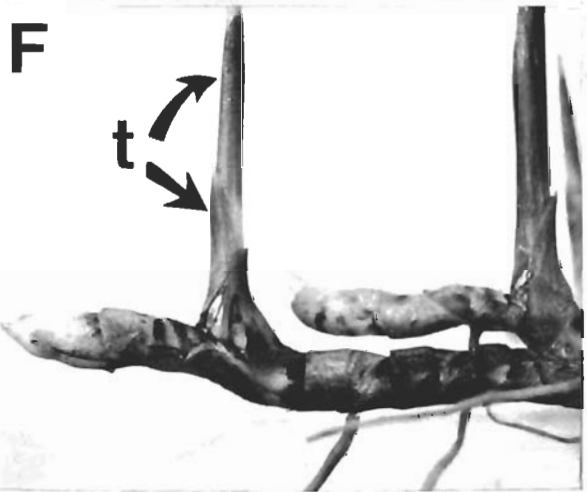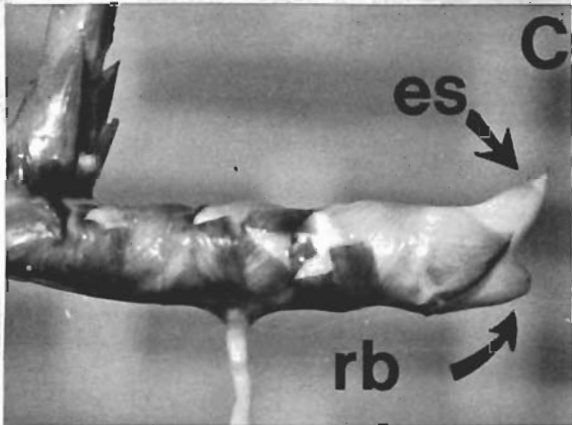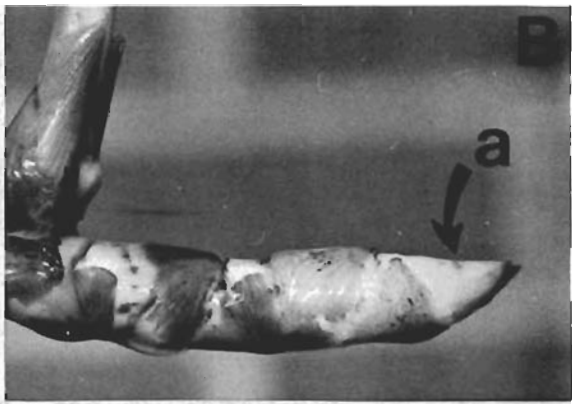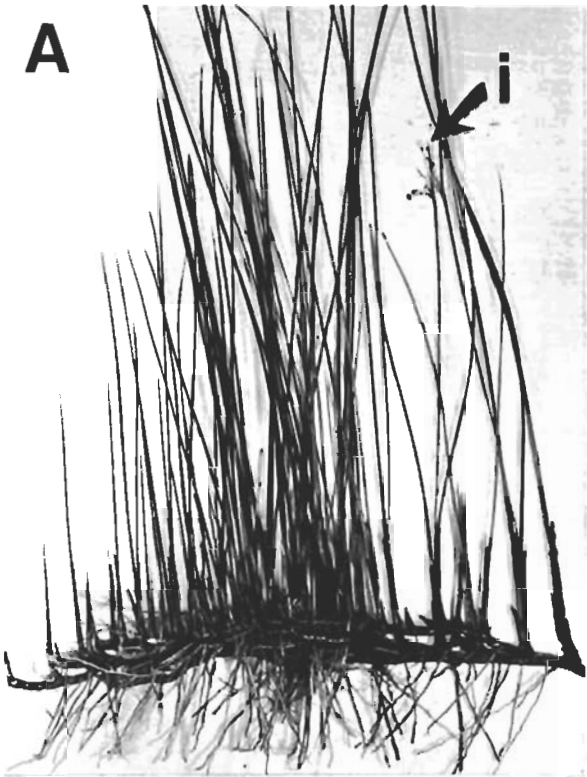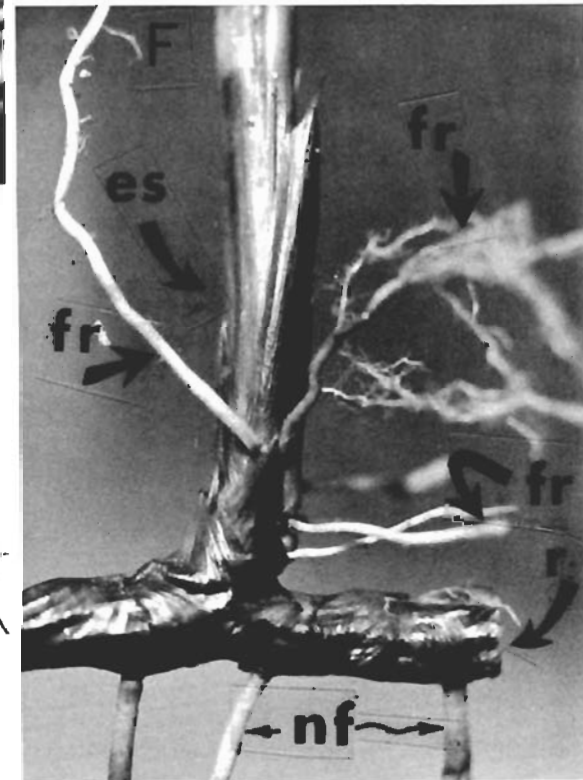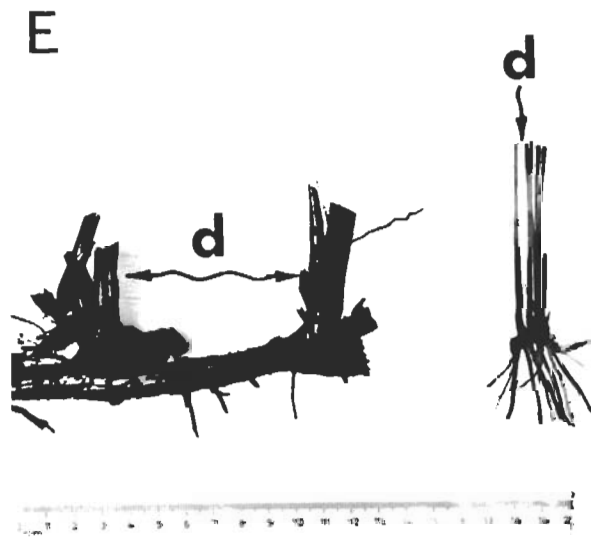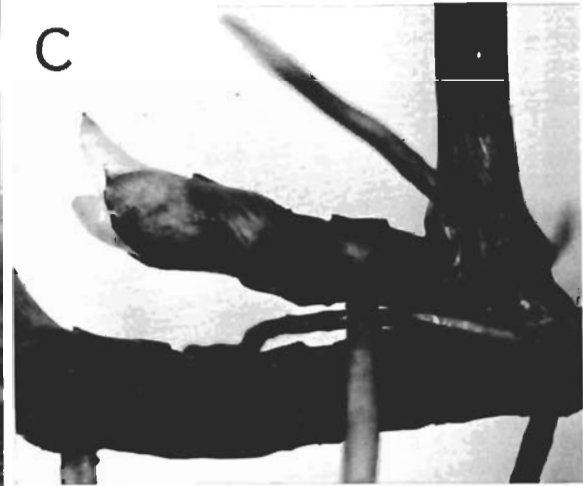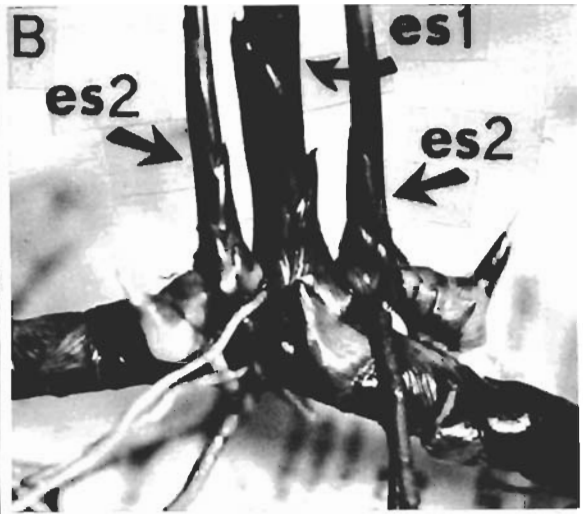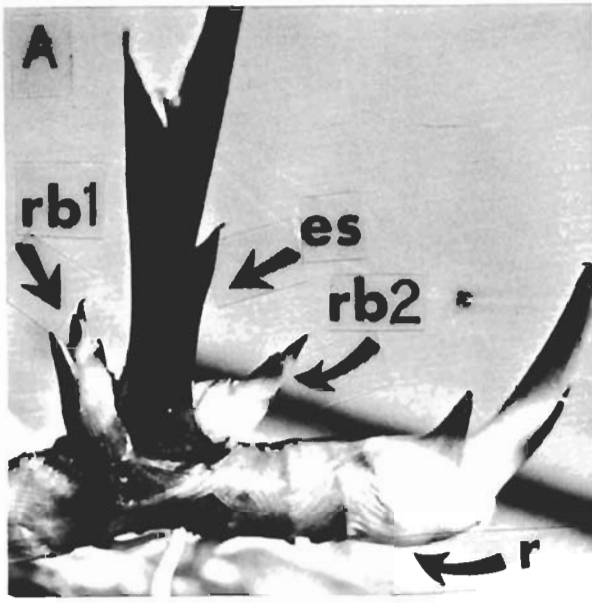
## The Roots

There are two types of roots found in *J. roemerianus*. One type branches frequently, is relatively small in diameter and somewhat stiff. The other type generally does not branch or does so infrequently. These roots are relatively large, succulent, deeply penetrating and consistently arise from the lower surface of the rhizome near the apex. The development of fibrous roots is somewhat delayed and restricted to the lateral surface (perpendicular to the plane of distichy) of the mature erect shoot (Figure 2-F).

## VEGETATIVE ANATOMY

### The Leaf

The mature leaf blade is symmetrical in cross section (Figure 3A). There is a single-layered epidermis with the outer cell wall thickened and heavily cutinized. Stomata are not recessed. The stomatal cavity or substomatal chamber occurs in the palisade at a depth of one to several cells. Procumbent protective cells line the substomatal cavity (Figure 3B and C).

The chlorenchyma is composed of six to seven layers of elongated palisade cells with slightly swollen, pointed ends. The cells, more or less perpendicular to the leaf surface, appear to radiate from sclerenchyma girders or strands which occur next to the epidermis in triangular or irregular patches in cross section. These strands are often close together, separated by the width of the stoma only (Figure 3C–F). Other strands of sclerenchyma, more or less rounded or oval in outline, are scattered in the central ground tissue especially toward the solid parenchyma leaf center where each is surrounded by a parenchyma sheath. Both inner sclerenchyma and outer parenchyma bundle sheaths surround the vascular bundles.

The vascular bundles generally occur in two or three rings in the cylindrical leaves. Large vascular bundles with two medium-sized metaxylem vessels on either flank occur in the leaf center. The smaller bundles occur outermost and may be arranged in two or more rings, some free in the central ground tissue of the culm. However, most of the vascular bundles are concentrated near the periphery of the leaf. The phloem of the vascular bundles is external to the xylem and the arrangement of the vascular tissue within the leaf resembles that of an atactostele. The phloem is frequently surrounded on the outside by sclerenchyma or thick-walled parenchyma cells. Fibers are often found in the phloem. A series of branching parenchyma cells radiate from the sclerenchyma girders to the vascular bundles. These cells are stellate, a highly specialized polyhedral cell type, and form transverse diaphragms or septa within the leaf (Figure 3D).

### The Culm

The flowering stem or culm is weakly developed and easily broken. Chlorenchyma occurs beneath the single layer epidermis. It is composed of irregular or rounded cells, two to three cells in thickness, and a few strands of sclerenchyma. These sclerenchyma girders are much smaller than those found in the leaf. The culm center is composed of continuous parenchyma. A series of radiating diaphragms of stellate, lobed cells or branching parenchyma are also found in the culm. The vascular bundles are fewer in number but larger in size in comparison to those of the leaf (Figure 4A and B). However, the orientation of the phloem is the same as for the leaf, being external to the xylem. The stomata are not sunken. Protective cells are found lining the substomatal cavity. The isodametric cells of the chlorenchyma are loosely arranged, which allows for the presence of air cavities (Figure 4C and D).

### The Rhizome

The abaxial side of the rhizome scale or cataphylls contains an epidermis covered by a thick layer of cutin. The epidermis of the scale is one cell in thickness, but the cells are very large. A parenchyma layer from several to 20 cells thick may be found between the upper and lower epidermis. The rhizome has an epidermis of one cell in thickness which often contains lignin. Under the epidermis occurs a many-layered hypodermis which generally varies in thickness along a single rhizome or between rhizomes of different habitats. The outer cell layers of the hypodermis are often lignified and filled with an unidentified material. Lignification accompanied by apparent suberization is pronounced in older rhizome portions. Under the hypodermis is a thick layer of loosely arranged parenchyma, considered to be cortex. The innermost layer of the cortex is a single endodermoid layer. In older portions of the rhizome, endodermoid cells have thickened inner walls. A pericycle, a layer of parenchyma

Figure 2. Vegetative morphology of *Juncus roemerianus*. 2A. Erect shoot and associated rhizomes and rhizome buds. Rhizome (r) was formed simultaneously with erect shoot (es). Rhizome bud (rb1) arises dorsally on the rhizome slightly behind the erect shoot (es). Rhizome bud (rb2) arises from the erect shoot. Note that the buds at rb1 and rb2 are forming erect shoots immediately after being formed. 2B. Erect shoot (es1) and associated erect shoots (es2) which arose from buds as described at A. 2C. Secondary rhizome developing erect shoot and rhizome bud which forms a further unit of the sympodium. 2D. Proliferation of erect shoots on colonizing plants growing without competition. Note that rhizome buds form erect shoots immediately. This example shows that elongated rhizomes between erect shoots are not formed in all instances. 2E. Distance (d) between erect shoots of mature plants varies between habitats. The segment of rhizome on the left has about 14 nodes and internodes separating erect shoots. This plant grew under conditions which apparently favored vegetative reproduction. The leaves were over 7 feet in length. The segment on the right has only a few nodes and compressed internodes between erect shoots. This plant grew under hypersaline conditions. 2F. Location of fibrous roots (fr) on erect shoot (es). These roots generally arise perpendicular to the plane of distichy on the lateral side of the erect shoot. Nonfibrous (nf) or anchoring roots arise from the ventral surface of the rhizome.
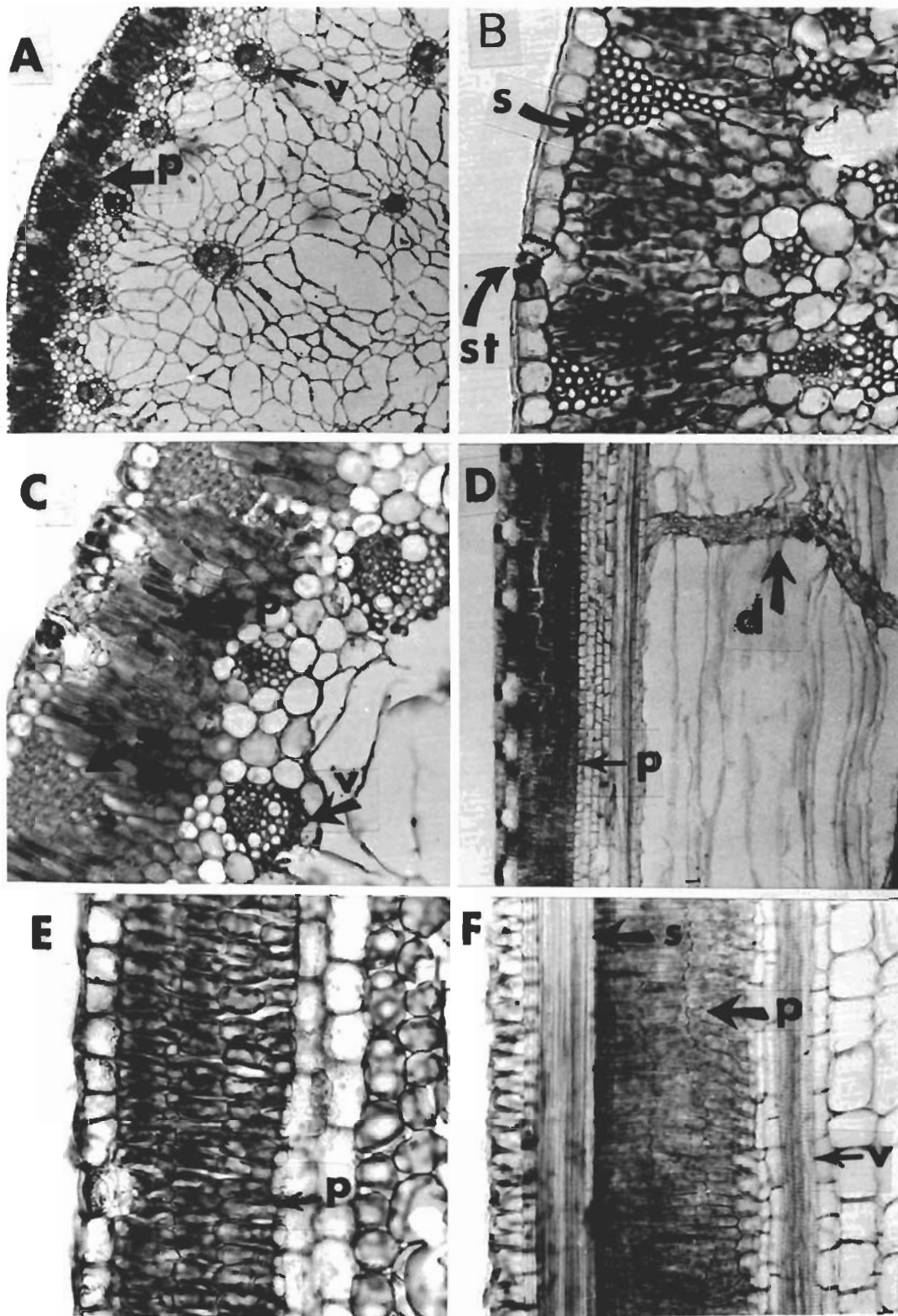
Figure 3. Anatomy of the leaf of *Juncus roemerianus*. 3A. Transection of leaf. Note the thick layer of palisade cells (p) forming chlorenchyma and vascular bundles (v). 3B. Leaf cross section showing sclerenchyma girders appressed against the epidermis and stoma (st) Note the procumbent protective cells lining the substomatal chamber. 3C Transection of leaf showing general arrangement of palisade cells (p) between sclerenchyma girders (s) and stomata (st). Vascular bundle (v) gives general view and shows phloem oriented external to the xylem. 3D. Longitudinal section of leaf showing a series of stomata on the extreme left underlaid by palisade cells (p). A diaphragm (d) or septum of stellate cells or branching parenchyma (polyhedrals). 3E and F. Longitudinal sections showing the regular arrangement of palisade cells (p), sclerenchyma girder (s) and vascular bundle (v).
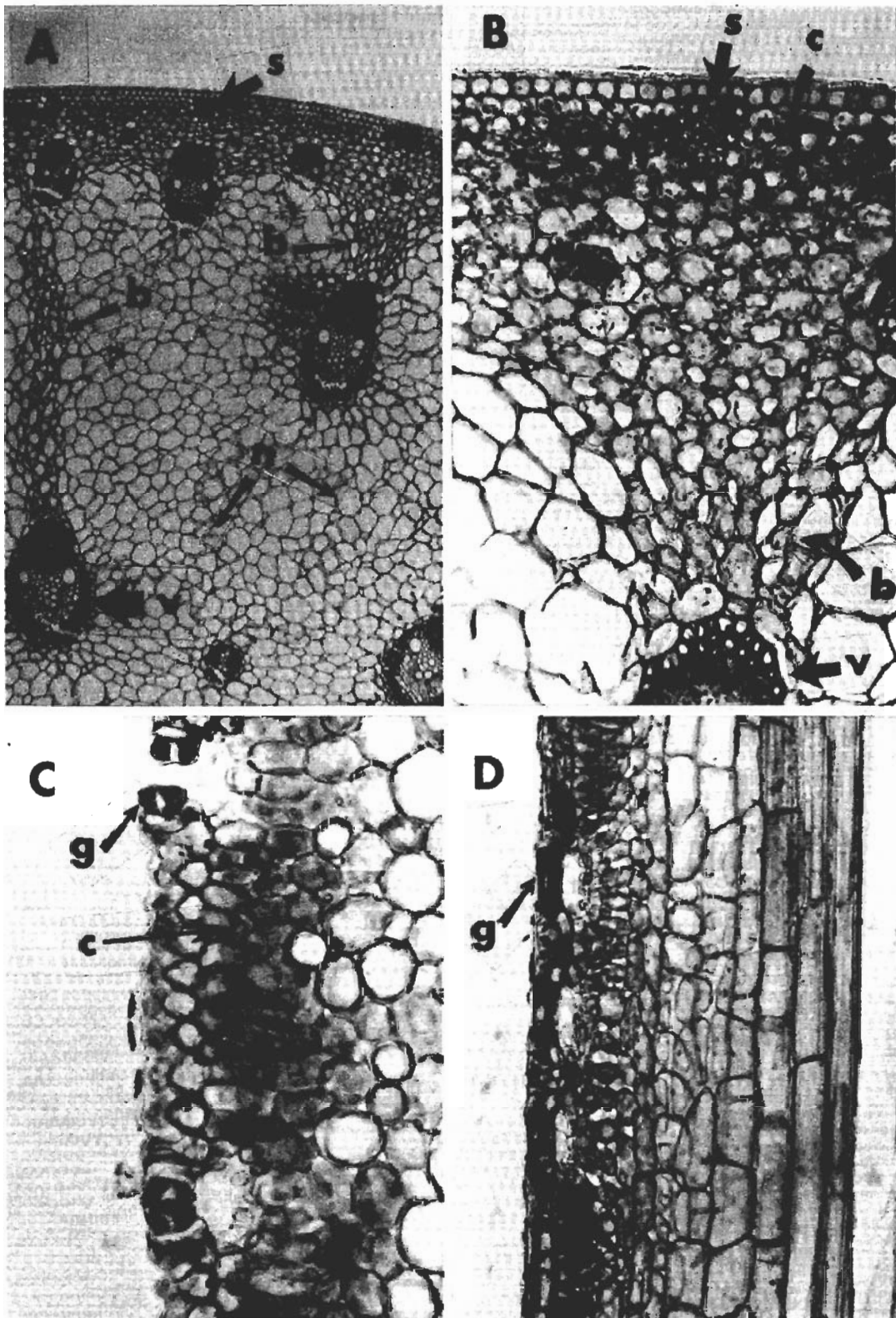
Figure 4. Anatomy of the culm of *Juncus roemerianus*. Transection of culm. Note arrangement of vascular bundles (v), diaphragms of stellate cells or branching parenchyma (b) and non-branching parenchyma (n). Sclerenchyma girders (s) are very small in comparison to those of the leaf. 4B. Close view of leaf in cross section showing sclerenchyma (s) and absence of palisade cells. Irregular or rounded cells form a thin layer of chlorenchyma (c). Note stellate cells (b) of diaphragm and extension to vascular bundles (v). 4C. Greater magnification of leaf cross section showing stomata with guard cells (g) and thin layer of chlorenchyma (c). 4D. Longitudinal section of leaf showing orientation of stomata and guard cells (g). Note loose arrangement of chlorenchyma.

tissue two to five cells in thickness, occurs immediately inside the endodermal layer. The center of the rhizome contains numerous amphivasal vascular bundles surrounded by parenchyma cells. Generally more vascular bundles are found near the outer portion of the stele than in the center. The smaller vascular bundles, often tortuously fusing or dividing, occur immediately to the inside of the pericycle. The central ground tissue is parenchyma (Figure 5A–C).

### The Roots

Although there are two types of roots, based on general morphology, no major anatomical differences were noted in comparing the two types. The roots have an epidermal layer one cell in thickness. The cortex is composed of radiating plates of cells separated by air spaces or lacunae. The outer part of this cortex is composed of a layer of hexagonal cells, three to nine cells in thickness. The inner part of the cortex is composed of a layer of rounded, thin-walled cells, which becomes thicker in older roots. This layer is three to eight cells thick. The endodermis is one cell in thickness, with very thick inner and anticlinal walls and thin outer walls. A pericycle, a layer one to three cells in thickness, occurs immediately within the endodermis. Phloem persists in mature roots as inconspicuous patches pressed against the pericycle. The entire center of the root appears to be composed of xylem. However, small, thick-walled cells which may be sclerified parenchyma, compose the central portion of the xylem and from 1 to 24 large vessels arranged in a ring occur in the outer portion of the stele where they are sometimes accompanied by a central metaxylem vessel in larger roots (Figure 5D and E). Individual metaxylem vessels may be surrounded on the outside by one layer of flattened tracheids (Figure 5F–G).

### DISCUSSION

In an earlier account it was suggested that *J. roemerianus* possesses monopodial branching (Eleuterius 1975). This was based on early stages of development in mature rhizome apices which showed where the meristem divided equally or nearly so with the resulting dorsal meristem often slightly larger than the ventral. The lower meristem gives rise to the dominant axis, the rhizome. In most cases the horizontal stem clearly exceeds the development of the erect stem. This prevailing condition suggested that two shoots had been initiated simultaneously, the horizontal shoot or rhizome being indeterminate. The branching is thus monopodial. Subsequently, a more detailed investigation showed that the

earlier supposition was incorrect and that sympodial branching in most mature plants of *J. roemerianus* involved precocious rhizome bud formation at the rhizome apex. This precocious bud formation is followed by vigorous rhizome growth, thus obscuring the clear-cut example of sympodial branching exhibited by immature and certain mature plants. The elongated rhizomes formed between the erect stems are peculiar and unique since in most species of *Juncus* where branching is distinctly sympodial the rhizome segment between erect shoots is rather short, resulting in a clumped habit. This is an important vegetative characteristic which accounts, in part, for the domination of *J. roemerianus* over large areas of salt marsh.

Sympodial branching implies that the plant is composed of units which are determinate and that further growth continues from axillary buds. In *J. roemerianus,* buds consistently arise in the axils of scale leaves on the ventral surface of the rhizome and frequently in the axils of transitional and foliage leaves on the erect shoot. Richards and Clapham (1941) state that the continuation bud consistently arises in the axil of the second scale leaf of *Juncus inflexus.* Anderson (1974) states that it occurs in the ninth scale leaf of *J. roemerianus.* However, I find the ventral scale leaf axil, in which the continuation bud occurs, to be highly variable. Sometimes it occurs immediately at the first node (where one node separates the erect shoots), while in other material the bud may be found in the axil of the eighteenth scale leaf (18 nodes separating the erect shoots). Thus, the formation of erect shoots and rhizome buds apparently does not occur after any fixed number of nodes. The number of rhizome nodes between erect shoots varies among plants from different localities and habitats of *J. roemerianus.*

In some populations of *J. roemerianus* rhizome growth is suppressed but the leaves are very long. In other areas the leaves may be relatively short, but rhizome growth is extensive. Various combinations of growth patterns exist in different habitats. In some areas of relatively low salinity, plants are often very robust with leaves over 7 feet in length, whereas, in hypersaline areas the plants are dwarfed (less than 1 foot). Whether this variation in the size of these plants is a response to environmental factors or due to genetic control remains unclear. However, data from reciprocal transplant experiments suggest that ecotypic adaptation may exist within *J. roemerianus.* Reduced plant size and increased vascularization of internal tissues is characteristic of plants which grow under saline conditions. However, the internal anatomy of various plant structures remains relatively constant. In dwarf plants the internal

**Figure 5.** Anatomy of the rhizome and roots of *Juncus roemerianus.* Transection of young rhizome showing arrangement and general appearance of tissues. The epidermis is a single layer of cells. The hypodermis (h), cortex (c) and endodermoid layer (e) are shown. The stele is composed of scattered amphivasal bundles. 5B. Transection of older rhizome showing well developed tissues. Note the lignified hypodermal cells (h) which may contain suberin. The cortex (c) and endodermoid layer (e) are well developed. The amphivasal bundles are well defined and are tightly appressed against the pericycle. 5C. An individual amphivasal bundle of rhizome stele. 5D. A cross section of a root. Note the large lacunae of the inner cortex, thick outer cortex and the relatively small vascular stele. 5E. Greater magnification of cross section showing detail of endodermis and vascular stele. Note the thick inner and anticlinal walls and thin outer walls of the cells of the endodermis. The metaxylem vessels are arranged in an outer ring. 5F. Another section of a root showing the endodermis with cell walls thicker than shown in E. This thickening appears to occur with age. 5G. Metaxylem vessel surrounded by flattened tracheids.
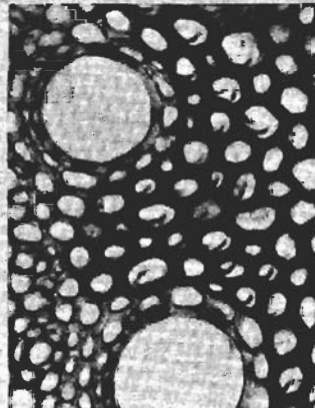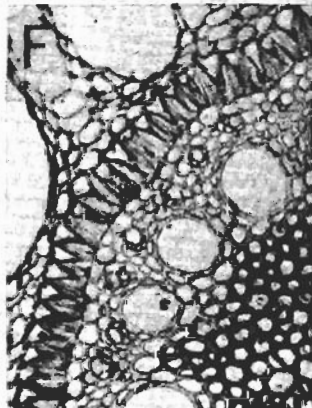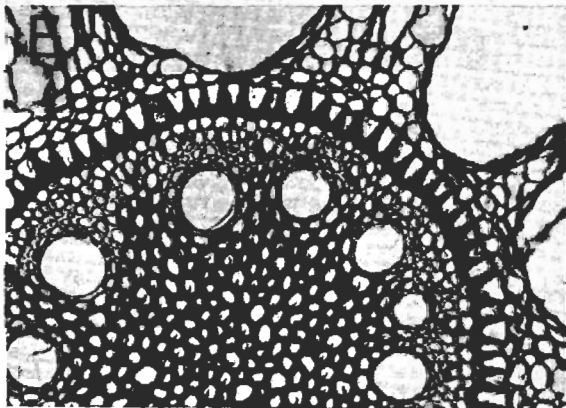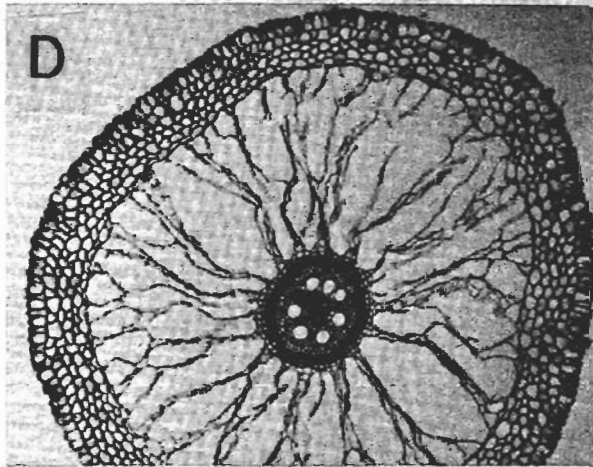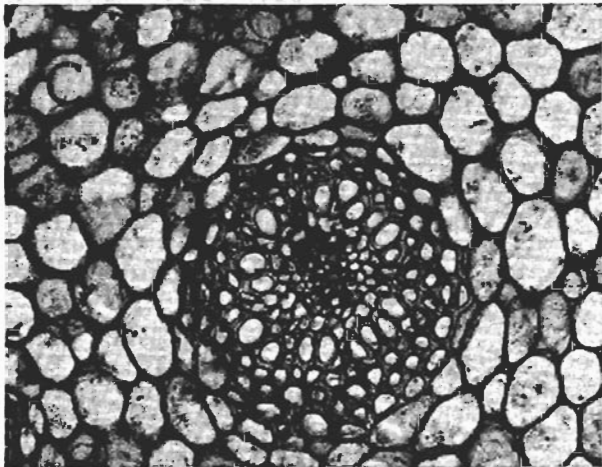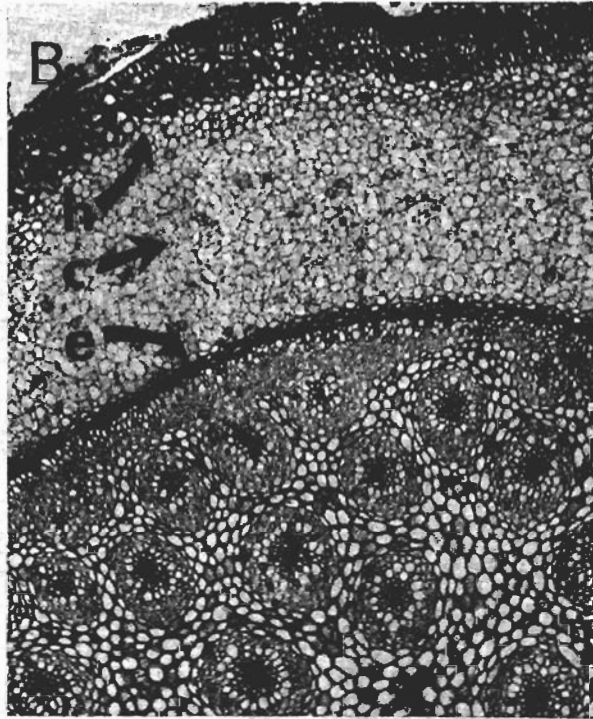
tissues are correspondingly reduced with an obvious reduction in the amount of parenchyma which occurs in all plant organs. The amount of parenchyma is partially restored in new organs of dwarf transplants when they are taken from hypersaline marshes and grown under low salinity.

The occurrence of stellate cells in the pith of the cosmopolitan *Juncus effusus* has been described in detail by Maas Geesteranus (1941). In *J. roemerianus, Juncus maritimus* Lam. and *Juncus acutus* L. these stellate cells form diaphragms and are regarded as a secondary development in the more advanced species (Buchenau 1906). Diaphragms have been found in other water plants (Kaul 1971, 1973, 1974) associated with air chambers which provide internal ventilation. These diaphragms probably give strength without rigidity (Snow 1914; Williams and Barber 1961).

Several morphological and anatomical features are apparently related to water regulation. These include the presence of lignin and possible suberin in the outer layer of the hypodermis and cortex of the rhizome and roots, the well-developed endodermis of the roots and endodermoid layer of the rhizomes, the heavy cutinization of the rhizomes, scales and foliage leaves, and the fibrous leaves. Clements (1907) stated that in grasses and sedges the presence of large amounts of sclerenchyma in the leaves renders water loss difficult.

Internal anatomy has much use in taxonomic work. The presence of pith in the leaf was the characteristic used by Buchenau (1906) in defining *Juncus* subgenus *Thalassi.* Raunkiaer (1895) placed *J. maritimus* in a separate category because the vascular bundles of the leaf and culm are found throughout the culm and leaf center. Adamson (1925) and Cutler (1969) showed that the leaf anatomy of *J. maritimus* and *J. acutus* are essentially the same. Anatomically *J. roemerianus* resembles these two species of *Juncus* which have solid piths with vascular bundles. The chief anatomical differences which exist between *J. maritimus, J. acutus* and *J. roemerianus* are found in transverse sections of the leaf.

The detailed morphological and anatomical characteristics of *J. roemerianus* described in this paper may have taxonomic value in diagnostic work, especially where hybrids are concerned or suspected (Stace 1970; Eleuterius 1975). However, no differences in vegetative anatomy were noted within *J. roemerianus* when plants which produce perfect and pistillate flowers were compared (Eleuterius and McDaniel 1974).

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