The shoot apex of Casuarina (Casuarinaceae)

by

E. M. Flores*

(Received por publication February 20, 1978)

Abstract: The shoot apex of *Casuarina* has a uni-layered tunica. The corpus grades into a peripheral zone and a central zone which forms the pith. The embryonic shoot is conspicuously developed and exhibits several leaf primordia. Leaves are whorled, scale-like, linear to lanceolate and mostly uni-veined. Except in their distal portions, the leaves of a whorl are concrescent along their lateral margins, forming a sheath which covers the base of the internode above the base of the whorl. The free apices are either valvate or laterally imbricate. There is a correlation between the number of leaf primordia produced and the size of the growth centers from which they develop. The area of the shoot apex in transection, as well as the perimeter of the circumference are not correlated with this phenomenon. The various concepts of the limits of the leaf in *Casuarina* are described

The Casuarinaceae usually grow in arid soils either along sea coasts in brackish areas, or inland on sand dunes or dry, sandy, upland savannas. The growth habit ranges from woody shrubs, as exhibited by *C. distyla* to large trees, as *C. cunninghamiana,* which attain heights of twelve to 30 m. The plants produce monopodial, acrotonous and radial stems with rough, persistent, and furrowed bark. This study of the shoot apex of *Casuarina* was undertaken to answer the many problems discovered by previous investigators (Loew, 1865; Boodle and Worsdell, 1894; Morini, 1894; Rao, 1972).

MATERIAL AND METHODS

Material of the shoot apices of embryos of *C. stricta, C. litorea, (C. equisetifolia), C. glauca* and *C. cunninghamiana,* and the apices of terminal buds in branches and branchlets of *C. stricta, C. cunninghamiana, C. glauca, C. paludosa, C. poisso-*

---

* Centro de Investigación en Biología Celular y Molecular y Escuela de Biología, Universidad de Costa Rica. The study represents a portion of a dissertation presented to the University of California in partial fullfillment of the Ph.D degree.

niana, C. leucodon and C. deplancheana have been examined. Part of the material was collected in Australia and the neighboring islands by R. Coveny and provided to the writer by Dr. L.A.S. Johnson. Other specimens were collected by the late J.T. Buchholz in New Caledonia or by the writer in California.

Materials for anatomical studies were fixed in F.P.A., F.A.A. (Johansen, 1940), Craf III (Sass, 1958) or formaldehyde gluteraldehyde (Karnovsky, 1965). A preliminary softening of the fixed material in fuming hydrofluoric acid (52%) was necessary. The tissues were then washed in water and dehydrated through a tertiary butyl alcohol series (Jensen, 1962) infiltrated with paraffin (56 C melting point) and embedded in Tissuemat (62 C melting point). Transverse, tangential and median longitudinal serial sections were made at varying thicknesses (8-12 μm) on an American Optical 820 rotatory microtome.

Embedded materials which were difficult to section were cut to expose the tissue and then soaked in distilled water for one to four days, or in a mixture of one part glycerin to one part of 95% ethyl alcohol for a period of two to three weeks before cutting.

Sections of meristems and mature tissues were stained with safranin, tannic acid and orange G (Sharman, 1973) or Harris' hematoxylin, safranin and fast green. Some sections of young material were stained with fast green and 3% aqueous solution of phloxine (Jacobs and Morrow, 1957). Shoot apices were cleared (Sporne, 1948; Bisalputra, 1960) to supplement the serial sections in studying the vascular system. An American Optical Microstar 10 research microscope fitted with polarizing accessories and a 4 x 5 camera back adapter was used to make the photomicrographs using Kodak Ektapan 1462 film.

OBSERVATIONS

The species present striking variations in size and habit in response to habitat differences. In some, the height is conspicuously reduced, especially under adverse edaphic conditions; the tickness and length of branchlets and the length of the internodes may also be strongly modified (i.e. *C. stricta, C. cunninghamiana).*

Each year several wiry, rigidly erect (i.e. *C. rigida, C. cunninghamiana)* or pendulous (i.e. *C. stricta)* assimilatory branches (per Metcalfe and Chalk, 1950) develop from buds along the tertiary and quaternary branches. Any or all nodes may eventually produce branchlet buds. Later, the axillary buds, formed at the nodes of the assimilatory branches, give rise to numerous branchlets. Generally, two or three or sometimes four buds develop at each node of the assimilatory branch at different times during the growing season (Fig. 1). The internodes of the assimilatory branches frequently do not elongate, or elongate very little, when the production of branchlets occurs. The internodes of the branchlets grow at different rates, but they are always longer than those of the assimilatory branches.

In some species, as *C. poissoniana,* which have only four leaves at each node, axillary buds develop acropetally for three to four succesive nodes. No buds develop in the next two to three nodes. All of the axillary buds at one node show similar rates of growth. Growth of an assimilatory branch giving rise to branchlets terminates four or five nodes above the area of axillary bud development. The terminal bud becomes dormant and the last four leaves formed develop as thickened cataphylls.

The leaves are scale-like, often green and occur in whorls of four to sixteen. The number of leaves in a whorl varies considerably in the different species and is not constant within the same species, nor even on the same plant. A population of twelve trees of *C. stricta* growing at the Santa Barbara Airport, California, was analyzed for this variation. The branchlets of each tree were examined and the number of leaves per node varied from eight to thirteen on the same branchlet. Trees producing pistillate inflorescences showed a tendency to have a higher number of leaves per node than those of the developing staminate inflorescences. In any case, a higher leaf number per node is correlated with wider internode diameter and vice versa. A population of five trees of *C. glauca* growing in Santa Barbara, California, presented similar variability, although the leaf number varied from ten to sixteen.

The leaf shape, linear to lanceolate, also differs among species, but remains more constant within the same species. The laminae are symmetrical and the leaf apices are attenuate in most species, but in *C. deplancheana, C. poissoniana, C. leucodon* and *C. nodiflora* the leaf apices are acuminate.

Each leaf has one vein except in *C. deplancheana, C. poissoniana,* and sometimes *C. nodiflora* and *C. leucodon,* where each is three-veined. Except in distal portions, the leaves of a whorl are concrescent laterally. The free apices are either valvate or laterally imbricate.

The whorled leaves of each succeeding node alternate with those below and above, as do the internodal furrows and the ridges. In four of the species studied, *C. deplancheana, C. leucodon, C. poissoniana* and *C. nodiflora,* the furrows were glabrous and the leaves had shorter free leaf-tips. These species also tend to have opposite and decussate leaves on a quadrangulate stem (Fig. 2).

Casuarina stricta has been selected as a model for a description of the embryo. Apices in all four species studied have the same basic structure; however, slight variations in size are found and summarized in Table 1. Table 1 also lists the number of leaves found in the first whorl below the apex, the percentage of shoot area (as seen in cross section) occupied by the whorl and the area occupied by each individual leaf. The values obtained show that slight variations in apical width (diameter) are not significant, whereas the number of leaves per whorl is significant. The greater the number of leaves per whorl, the smaller is the percentage of the shoot apex surface used to produce the whorl and the farther they are inserted from the apex.

The shoot apex of the embryo in *C. stricta* is oval in transection with diameters of 86 μm and 120 μm respectively, and stands 72 μm above the base of the first leaf primordium. The apices have a uniseriate tunica and a corpus. The tunica initials and the central zone in the corpus are densely stained cells with large nuclei. A pith rib meristem and a peripheral meristem can be discerned at this stage. The leaf primordia arise low on the periphery of the apical meristem and the first periclinal divisions take place in the three external layers of the corpus.

The size and shape of the apical meristems of the branchlets vary with the diameter of the shoot, the time of year, and aparently with the pattern of leaf production. The apices are dome-shaped medianly and exhibit similar zonation in all of the species. At the maximum plastochronic phase, the apex of a branchlet of *C. stricta* attains a diameter of 96 μm in transection and a height of 43 μm above the first leaf primordium. Size variations between species are tabulated in Table 1.

In the branchlets the apices exhibit a one-layered tunica (Fig. 4) and a corpus which contains a mass of central mother cells darkly stained and similar to the initial cells of the tunica layer. This layer undergoes only anticlinal divisions and maintains its individuality throughout all stages.

Cells derived from the corpus initials produce a central pith rib meristem and a peripheral meristem which are increased in width by periclinal divisions in C_1. The pith rib meristem is a wide zone containing larger cells than those of the initials. Its cells are vacuolated and lightly-staining, although some cells show a dark red or brown stain absorbed by the (yet undetermined) phenolic substances contained within the vacuoles. The peripheral meristems also exhibit darkley-staining cells which are much narrower, and sometimes even more elongate than those of the pith rib meristem. Strands of procambium derived from the residual meristem are differentiated above the second node (Fig. 4), approximately 130 μm below the apex. Further development gives rise to a narrow cortex (Figs. 3,5,6) outside the stelar vascular bundles which are differentiated at about the same time.

In the Casuarinaceae, the cells of the cortex become vacuolated later than those of the pith. The cortex is at first not differentiated from the future vascular region. The same phenomenon was found by Golub and Wetmore (1848) in *Equisetum arvense* and by De Sloover (1958) in *Taxus baccata.* According to Esau (1965), this is a common pattern found in small-leaved gymnosperms and dicotyledons.

In the species of Casuarinaceae examined, the youngest whorl of existing leaf primordia has no identifiable procambial trace. It is in the second whorl below the apex that the most distal procambial traces appear. In dormant buds, the procambial strands may frequently extend down to the third or fourth whorl below the apex. The apices of the seven species observed have the same characteristics described for that of *C. stricta.* The three or four tunica layers described by Rao (1972) in *C. equisetifolia* (= *C. litorea)* were not observed in the specimens sectioned. The apices of the branches are similar to those of branchlets, although the former attain greater diameters.

The vegetative apices of casuarinaceous plants gradually change from the conical shape of the embryo to the rounded dome-shaped apex found in the branches and branchlets. Also, the apex height becomes reduced in branches and branchlets (see Table 1).

Origin of cataphylls and leaf primordia: Although the outer axial tissue in the internode immediately below a leaf attachment closely resembles the mesophyll of the leaf above in structure and arrangement, rather than cortical tissue, the writer considers a leaf to be strictly the protuberance which originates from the shoot apex. The concept of "phyllichnium" of Loew (1865) applied to Casuarinaceae leaves will be discussed later.

The inception of lateral growth occurs during the maximal and terminal phase of a plastochron and gives rise to the leaf primordia which emerge on the periphery of the apical dome. Leaf and cataphyll primordia are initiated by periclinal divisions in C_1, C_2 and deeper layers of the corpus (Fig. 4). The periclinal divisions appear first in the C_1 layer although eventually these cells appear to be dividing at a rate comparable to other cells of the corpus. Both anticlinal and oblique divisions occur in the leaf initiation area. The tunica divides only anticlinally.

When leaves are produced in a decussate arrangement around the apex (i.e. *C. poissoniana),* the leaf primordia develop at faster relative rates than those in whorls. Whorled leaves are initiated by separated growth centers, followed later by the formation of a continuous ring of growth due to the extension of cell divisions to either side of each leaf primordium. The ring takes on various shapes according to

TABLE 1

Size variation in the apices of embryos, branchlets and branches of some species of the Casuarinaceae[a]

Species	Embryo apex (μm)	Diameter branchlet apex (μm)	No. of leaf[b] primordia per whorl	% of shoot[c] area per leaf	% of shoot[d] area per whorl	Branch apex
C. stricta	W86 x 120[e]	106	10	0.65	6.45	119
	H 72	48				52
C. litorea	W78 x 106	84	7	1.84	12.90	110
	H 68	43				46
C. cunninghamiana	W82 x 109	85	7	1.84	12.90	92
	H 65	40				43
C. glauca	W88 x 122	112	14	0.24	3.36	123
	H 67	45				53
C. paludosa	W -	87	7	1.84	12.90	91
	H -	41				43
C. nana	W-	66	4	9.08	36.34	68
	H -	35				37
C. leucodon	W -	65	4	0.08	36.34	69
	H -	41				46
C. deplancheana	W -	80	4	0.08	36.34	107
	H -	51				58
C. poissoniana	W -	71	4	9.08	36.34	74
	H -	48				53

[a] The average of at least six apices per species examined.

[b] The No. of leaf primordia given corresponds to the first whorl below the apex.

[c] This value represents the % of the shoot area (transverse section) occupied by each leaf.

[d] This value represents the % of the shoot area occupied by the whorl as measured in the cross sections.

[e] W represents the width in the transections of embryo apices and the shoot diameter in branchlet and branches; H represents the height.

the number of leaves initiated per whorl; it may be quadrangulate as in *C. poissoniana*, or polygonal with a variable number of sides, as in *C. stricta* and other species, due to more active cell divisions in the regions below the developing leaf primordia. As seen in longitudinal section the ring of primordia is four to five cell layers in vertical depth (Fig. 4).

From the time of their initiation, the primordia are dorsiventral and acrovergent over the shoot apex due to more rapid growth on the abaxial surfaces than on the adaxial (Figs. 3,4). The leaf blade continues growth acropetally; a rapid longitudinal growth of the leaf blades is maintained by active apical meristems as well as by intercalary divisions.

Periclinal and anticlinal intercalary divisions near the margins of each primordium result in the formation of a narrow lamina (Fig. 6). Many periclinal divisions and some anticlinal divisions are found in the median abaxial leaf side; this gives rise to the characteristic rib (Fig. 6). Similar divisions are found in the internodal ridges. During the development of the basal ring, forming the gamophyllous leaves, the cells in the furrows between contiguous laminae elongate transversely increasing the diameter of the ring.

Casuarina deplancheana, *C. nodiflora*, *C. poissoniana* and *C. leucodon* have shorter but wider free laminar tips than in the other species; this is correlated with a shorter period of activity in the leaf apical meristem and greater frequency of cell divisions near the margins of the leaf blade. Cell vacuolation in the abaxial side of a leaf primordium starts when the leaf is approximately 62 µm long and proceeds basipetally and adaxially. Leaf maturation is basipetal; cell enlargement continues basally even after cell division has ceased. Cataphyll primordia show a similar development and the same internal differentiation as that found in the leaf primordia.

Axillary bud development: The axillary buds are initiated in the axils of one to several leaves in the fifth node below the apex (Fig. 7). Each axillary bud starts its development when the subtending leaf primordium is approximately 480-500 µm long. Early vacuolation of the surrounding stem tissues delimits these small growth centers from the neighboring cells (Fig. 7,8). An axillary bud meristem divides in all planes at the beginning; later, it remains dormant during most of the winter season. The formerly dorsiventral shape of the young lateral shoot (Fig. 9) is followed very early by a radial symmetry (Fig. 10) after the first whorl of leaves is initiated. After this change of symmetry, a well-defined apical zonation like that found in the terminal shoot apex is present. Each bud produces several successive whorls of leaves, the first whorl produced commonly has two to three prophylls if the species is tetramerous (Figs. 9,10), or three to four prophylls in the species which have more leaves per whorl.

DISCUSSION

Loew (1865) distinguished a peripheral region in the shoot apex of the embryo of *C. equisetifolia* (= *C. litorea)*, which gave rise to the whorl of leaves and the vascular system. A central region formed the pith. Morini (1890, 1894) described the apex of the embryo in *C. quadrivalvis* (= *C. stricta)* as a mass in which it was possible to recognize only a central group of initial cells.

The writer's interpretation of the embryonic apices of *Casuarina* agrees with those of Loew (1865) but differs from those of Morini (1894). Morini stated that the embryo apex lacked any zonation and emphasized the opinion that the precocious differentiation of leaves in the embryo shoot influenced Loew (1865) to consider that zonation existed in the apical meristem of embryos. Embryo apices of the casuarinaceous species reach a very large size; similar embryo apices are also found in Elodea *(Anacharis canadensis)* and some gymnosperms.

Rao (1972), stated that the normal and fleshy stems of *C. equisetifolia* (= *C. litorea),* possessed apices with three tunica layers, and a tendency for the formatin of a fouth layer. The corpus was described as consisting of three layers of cells which gradually merge with the rib meristem. The apex appears to me to have only one tunica layer (per Schmidt, 1924). Observations of samples of several species make it apparent that the second and third layers frequently divide periclinally, adding cells to the corpus. The shoot apices of the branches exhibit the same pattern of zonation as the branchlets.

Initiation and early development of leaf primordia in the Casuarinaceae follow the pattern defined for most angiosperms (Foster, 1939; Esau, 1965; Kaplan, 1970). The several growth centers established in the peripheral zone are followed by a continuous circular meristem which elevates the whorl of free leaf-tips and the leaf sheath. As shown in Table 1, there is a correlation between the number of leaf primordia produced and the size of the growth centers from which they develop. The area of the shoot apex in transection, as well as the circumference, are not correlated with this phenomenon.

The small, univeined leaf primordium exhibits a short period of apical and marginal activity which results in a small narrow lamina. Abaxial, periclinal divisions produce a dorsal leaf rib, but similar divisions in the internode below each leaf elevate an internodal rib which is continuous with the leaf rib above. The continuous rib from an internode beneath a leaf, through the region of the leaf sheath and into the free tip creates an image of leaf continuity from the internode into the appendage.

The continuity of the ribs in the leaves and internodes was first observed by Loew (1865), who applied the term "phyllichnia" to these ridges, and who reported that each leaf whorl was fused to the stem throughout the length of the internode below the free appendages. Agreeing with Loew, Morini (1894) stated that in the embryos, "the leaves are adnate to the stem, and consequently, the concrescent growth of these two organs is initiated near the embryo apex and accentuated with the longitudinal elongation of the internode". Although Morini's observations were concerned only with the embryos of *C. quadrivalvis* (= *C. stricta)* and *C. equisetifolia* (= *C. litorea),*it is obvious that the development of the continuous rib from internode to leaf is a phenomenon widely exhibited by embryos, branchlets and branches in the Casuarrinaceae. Most of the tissue forming the ribs differentiates as chlorenchyma; the mesophyll of these ridges may have become progressively elaborated among the various species. This fact induced Metcalfe and Chalk (1950) to concur with the idea of Loew (1865) that a displacement of tissues within the adnate leaves had occurred as a result of their concrescence to the stem.

Saunders (1922) stated, as part of the Leaf-Skin Theory of the stem that the "leaf-skin" covering the stem is formed "by a downward growth and extension of the leaf primordium, which keeps pace with the extension of the central axis with which it is fused". Although it is difficult to understand fully what Saunders meant one might assume that she visualized that leaf bases developed basipetally in those leaves which appeared to be in lateral contact at insertions, as in the Casuarinaceae.

Troll (1939) considered that a leaf is a separate entity from a stem, and hence would be free of a stem except for its basal attachment. Presumably, utilizing Troll's concept, only a free leaf-tip and its part on of the leaf sheath below, which is separate from the stem, would be a leaf in *Casuarina*. Boke (1944) interpreted chlorenchymatous internodal ribs in Cactaceae as axial in origin.

Thus, the leaf-like nature of the internodal peripheral tissue is controversial; Troll (1939) and Boke (1944) considered such tissue as modified stem tissue; Saunders (1922) considered it the product of an elongation of leaf bases; Loew (1865) and Morini (1894) considered it the product of the adnation of leaf to the stem. Each is a different interpretation for the peripheral tissue below the free leaf blades, and, each excludes the others. Although recognizing that leaf and stem are difficult to separate, I prefer to consider the internodal ribs as axial in origin, and that the limit of a leaf is determined by its projections as a lateral appendage.

Due to the presence of chlorenchyma within the internodal ribs in *Casuarina* the term cladode has been used to refer to the branchlets and branches (Rao, 1972). Jackson (1928) defined a cladode or cladophyll as a "branch assuming the form and function of a leaf". Even when the photosynthetic process is carried on by the stem, it does not assume a leaf shape; it is radial and not bifacial as are typical leaves. The branches and branchlets differ from the true cladode, as in *Phyllocladus;* and, therefore, that term is not applicable to shoots in Casuarinaceae.

Axillary buds develop low on the shoot apex from tissue derived from a peripheral zone. Foster (1939) indicated that the axillary buds frequently arise in direct continuity with the shoot apex, but in the Casuarinaceae they do not show a close continuity with the apex.

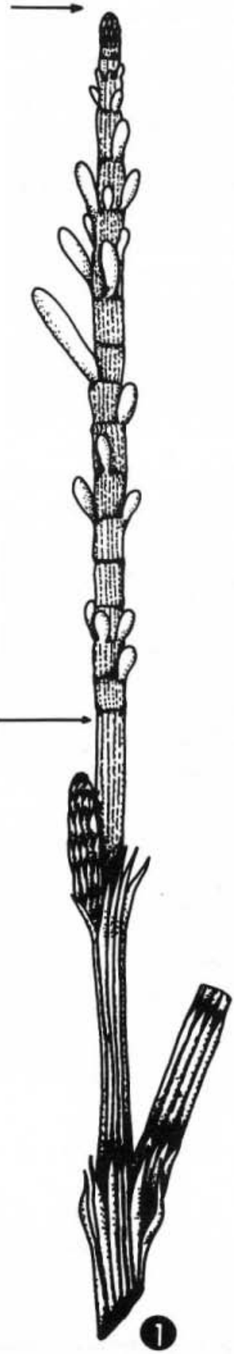
Commonly in angiosperms, procambial differentiation is associated with the youngest identifiable leaf primordium (Esau, 1965) and it develops acropetally and basipetally. The late development of procambium and its bidirectional differentiation in the shoots of *Casuarina* have been noted. Perhaps, these features are the results of the shoot reduction or the whorled habit. A similar pattern was found in dormant buds of *Abies concolor* (Parke, 1963).

ACKNOWLEDGMENTS

I thank L.A.S. Johnson, Royal Botanic Gardens, Australia, for providing part of the material for this research and for his invaluable help with species identification and to M.F. Moseley, D.R. Kaplan and I.B. Morrow for their critical reading of this manuscript.

Fig. 1 Schematic view of an assimilatory branch of *C. stricta: i,* region of branchlet development; whorls of leaves were removed at nodes. 20x.

Fig. 2 Schematic view of an assimilatory branch of *C. poissoniana* exhibiting the pattern of branchlet development. *ii,* lateral branchlets. 20x.



❶

❷

Se examinó los meristemas apicales de embriones, ramas y semillas de varias especies de *Casuarina*. El ápice del embrión es muy desarrollado y tiene varios primordios foliares. Las hojas son verticiladas, escamosas, lineares o lanceoladas y generalmente uninervias. Las hojas de un verticilo son concrescentes a lo largo de los márgenes de la lámina excepto en el extremo distal. Esta concrescencia forma una vaina que cubre la base del entrenudo inmediato superior al nudo en que se origina la misma; los ápices libres de las láminas son valvados o literalmente imbricados. Hay correlación entre el número de primordios foliares producidos y la talla de los centros de crecimiento de los que ellos se desarrollan. El área de ápice (sección transversal), así como el perímetro de la circunferencia, no se correlacionan con este fenómeno. Los varios conceptos de límites de la hoja en *Casuarina* son descritos y analizados de acuerdo con las observaciones.

LITERATURE CITED

Bisalputra, T.
1971. Anatomical and morphological studies in the Chenopodiaceae. II. Vascularization of the seedling. *Aust. J. Bot.*, 9: 1-19.

Boke, N. H.
1944. Histogenesis of the leaf and areole in *Opuntia cylindrica*. *Amer. J. Bot.*, 31: 199-316.

Boodle, L. A., & W. C. Worsdell
1894. On the comparative anatomy of the Casuarince with special reference to the Gnetaceae and Cupuliferae. *Ann. Bot. Lond.*, 8: 231-264.

De Sloover, J.
1958. Récherches sur l' histogénése des tissues conducteurs. II.- Le sens longitudinal de la différenciation du procambium, du xyléme et du phloéme chez *Coleus, Ligustrum, Anagallis* et *Taxus*. *Cellule*, 59: 55-202.

Esau, K.
1965. *Vascular differentiation in plants.* Holt, Rinehart & Winston. New York.

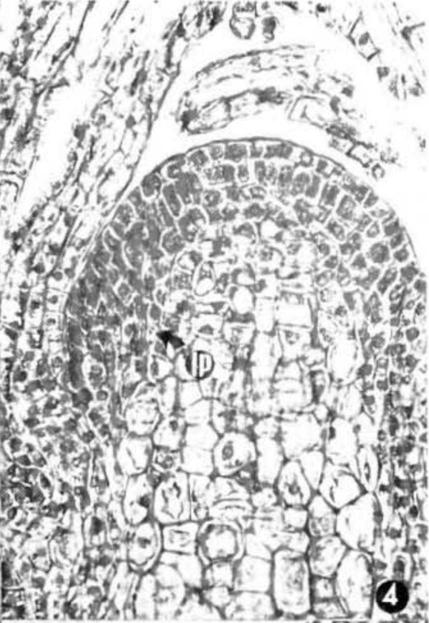
Fig. 3 Longitudinal section of a branchlet shoot of *C. stricta* showing the shoot apex and several nodes (with leaves). 210x.

Fig. 4 Median longitudinal section of a branch shoot apex showing the apical zonation and leaf initiation; *lp*, leaf primordium. 210x.

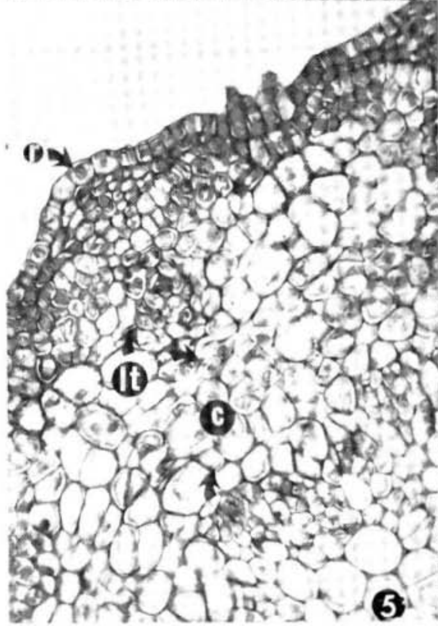
Fig. 5 Transverse section of a portion of shoot apex of *C. stricta;* C. narrow cortex; *lt*, leaf trace; *r*, rib. 210x.

Fig. 6 Transverse section of the whorled leaves of *C. stricta:* a, periclinal divisions in the median abaxial leaf side; b, anticlinal divisions in the abaxial leaf side. 210x.

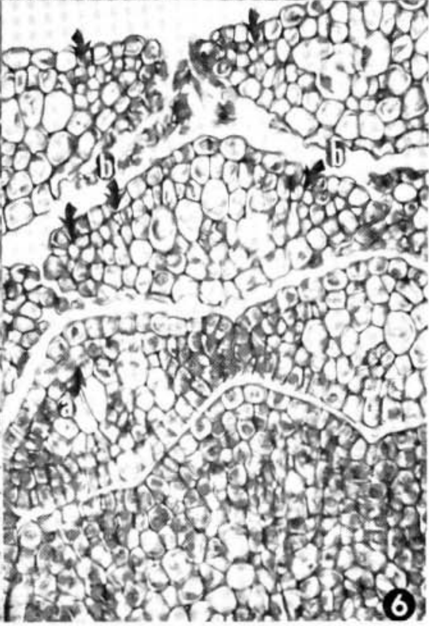
3



4



5



6

Foster, A. S.
1939. Problems of structure, growth and evolution in the shoot apex of seed plants. *Bot. Rev.*, 5: 454-470.

Golub, S. J., & R. H. Wetmore
1948. Studies of the development in the vegetative shoot of *Equisetum arvense* L. I. The shoot apex. *Amer. J. Bot.*, 35: 755-767.

Jackson, B. D.
1928. *A glossary of botanic terms*. Hafner Publishing Co., Inc. New York.

Jacobs, W. P., & I B. Morrow
1957. A quantitative study of xylem development in the vegetative shoot apex of *Coleus*. *Amer. J. Bot.*, 44: 823-842.

Jensen, A. W.
1962. *Botanical histochemistry*. W. H. Freeman. Berkeley.

Johansen, D. A.
1940. *Plant microtechnique*. McGrow-Hill. New York.

Kaplan, D.
1970. Comparative foliar histogenesis in *Acorus calamus* and its bearing on the phyllode theory of monocotyledonous leaves. *Amer. J. Bot.*, 57: 331-361.

Karnovsky, M. J.
1965. A formaldehyde-gluteraldehyde fixative of high osmolarity for use in electron microscopy. *J. Cell. Biol.*, 27: 137A-138A.

Loew, E.
1865. *De Casuarinearum caulis foliique evolution et structure*. Dissertatio inauguralis botanica. Berolini.

Metcalfe, C. R., & L. Chalk
1950. *Anatomy of the icotylendons*. Clarendon Press. Oxford. 2 Vols.

Morini, F.
1890. Anatomia del frutto delle Casuarinee. Ricerche Anatomiche sull embrione. *Mem. R. Accad. Bologna, Sci. Fis., Serie 5,* 1: 115-137.

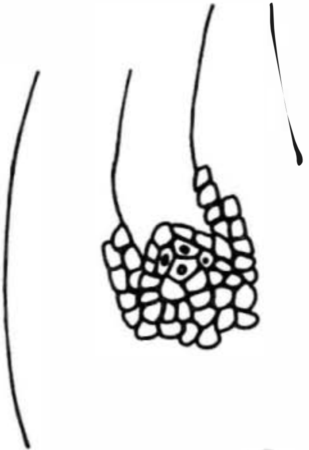
Morini, F.
1894. Contributo all' anatomia del caule e della foglia delle Casuarinaee. Momoirie I. *Mem. R. Accad. Bologna, Sci. Fis., Ser. 5,* 4: 685-736.

Fig. 7 Axillary bud initiation at node No. 16. 210x.

Fig. 8 Further bud development. 210x.

Fig. 9 Dorsiventral axillary buds with two or three prophylls in cross section. 130x.

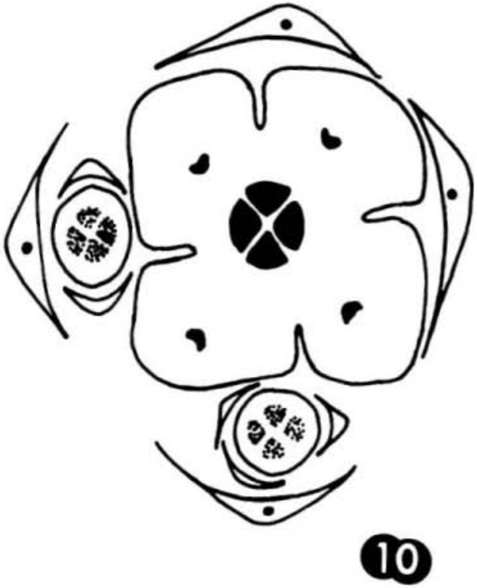
Fig. 10 Axillary shoots exhibiting radial symmetry after the first whorl of leaves is produced. 130x.



7

9

8



10

Parke, R. V.
1963. Initial vascularization of the vegetative shoot of *Abies concolor. Amer. J. Bot.,* 50: 464-469.

Rao, A. N.
1972. Anatomical studies on succulent cladodes in *C. equisetifolia* L. *Proc. Indian Acad. Sci. LXXVI Sec.,* 86: 262-270.

Sass, J. E.
1958. *Botanical microtechnique.* The Iowa State Univ. Press. Ames, Iowa.

Saunders, E. R.
1922. The leaf-skin theory of the stem: a consideration of certain anatomico-physiological relations in the spermatophyte shoot. *Ann. Bot.,* 36: 135-165.

Schmidt, A.
1924. Histologische Studien an phanerogamen vegetation spunkten. *Bot. Arch.,* 8: 345-404.

Sharman, E.
1973. Safranin, tannic acid and orange G for shoot apex, p. 121-126. *In* H.J., Conn, M.A. Darrow and V. M. Emmel. *Staining Procedures used by the Biological Stain Commission,* 3d ed. Williams & Wilkins, Baltimore.

Sporne, K. R.
1948. A note on a rapid clearing technique of wide application. *New Phytol.,* 47: 291.

Troll, W.
1939. *Vergleichende Morphologie der hoheren Pflanzen. Band 1. Vegetations-organe Teil 2.* Gebruder Borntraeger. Berlin.