MORPHOLOGY AND ANATOMY OF PHORMIUM TENAX FORSTER

by

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MORPHOLOGY AND ANATOMY OF PHORMIUM TENAX FORSTER

New Zealand flax, New Zealand hemp or phormium flax, *Phormium tenax* Forster, and mountain flax, *Phormium colensoi* Hook.f., were put to a variety of uses by the pre-European Polynesian immigrants to New Zealand. However, New Zealand flax was not known to the western world till its discovery in New Zealand by Captain Cook on his first voyage to the South Sea Islands in 1768-1771. On his second voyage in 1772-1775 Cook recorded the plant from Norfolk Island, with the remark that it appeared to be more abundant there than in New Zealand. Labillardiere, one of the naturalists accompanying the French expedition of 1791-1792, was probably the first to give a more detailed account of the plant than had previously been published (2, pp. 81-83).

The plant was first successfully established in cultivation at Kew Garden, London, and in many parts of Europe in 1789 (9, pp. 174-177). Subsequently, *Phormium* was introduced into many countries for the purpose of commercial fiber production, notably St. Helene, Kenya, Tanganyika, Natal, South Africa, Mexico, Brazil, Chili, Argentina, and Japan (38, p. 418). In the United States it has been planted principally in gardens as an ornamental, though it had been suggested that *P. tenax* could be established on a commercial scale in the Southwest in areas where irrigation water is available. Attempts have
been made to improve the plant with regard to its fiber content and method of cultivation. Mr. D. W. Fisher, U.S.D.A. and formerly stationed at Oregon State College, was probably the first to establish an experimental planting along the coast of southern Oregon in 1950. The investigation is being continued now by Mr. Stanton of the U.S.D.A., also stationed at Oregon State College. Experimental plantings have also been made along the coast of northern California by Dr. J. M. Webber, U.S.D.A., now stationed at the University of California, Berkeley, California.

The first export of fiber from New Zealand was made in 1850, and for many years this was the only source. The introduction of Phormium into other countries has rapidly increased the world production of phormium fiber which amounted to 36 million pounds in 1951 (38, p. 419). New Zealand was estimated to have produced 11.0 million pounds, Argentina 15.0 million, St. Helene 2.0 million, Chili 1.8 million, and Japan 6.0 million pounds.

The principal uses of phormium fiber are for cordage and bagging fabrics. In South America the fiber is also used for shoes, mats and similar items, and the Japanese use the fiber to make an artificial silk material (38, pp. 419-420). In Africa the plant is considered to be a good soil renovator and is used to reduce erosion. The leaf pulp is also used as food for cattle (28, pp. 194-195).
Phormium was classified by earlier botanists and even by some recent reviewers (4, pp. 773-774; 7, pp. 320-324; 9, p. 112; 18, pp. 286-287; 32, pp. 100-105) as a genus in Liliaceae. Hutchinson (23, pp. 151-154) removed Phormium, Yucca, Dracaena, and Agave from Liliaceae and established a new family, Agavaceae, primarily on the basis of the woody caudex and arborescent habit of the plants. He stated that the Agavaceae "is not clearly marked by any one character from the Liliaceae, and is based mainly on habit", and that "it may be regarded as a family composed of the most advanced tribes formerly included in the Liliaceae and Amaryllidaceae."

Phormium has been considered by various authors to be comprised of about eight different species. However, many of the species epithets have been treated by the editorial staff of "Index Kewensis" as synonyms of presumed valid names (19, p. 503; 20, p. 326; 21, p. 211). Bentham and Hooker, in their "Genera Plantarum", considered that Phormium consists of two species, P. tenax Forster and P. colensoi Hook.f. (4, p. 773).

Generally P. tenax is considered to be the species of commercial importance and is distinguishable from P. colensoi in that the former has stiffer upright leaves. The most striking difference is that the seed pods of P. colensoi are twisted and droop on the seed stalk, whereas the pods of P. tenax are straight (9, p. 172).
Nevertheless, polymorphism of *Phormium* has been indicated by many workers (2, p. 205; 11, p. 127). Plants often may be seen growing side by side in a swamp in New Zealand, with the leaves of one absolutely straight and stiff from butt to apex, while in the other the whole upper part of the leaf hangs vertically downward, and all intermediates between these extremes are known (2, p. 205). Cross reported that in certain localities in New Zealand an unbroken series of forms exists that connect the two groups (10, pp. 61-66). One group is broadly characterized by large size, upright habit, strong fiber, and erect pods, while the second is distinguished roughly by its small size, lax habit, weak fiber, and drooping pods. In the "Manual of New Zealand Flora", Chesseman notes that the description of *Phormium* species cannot be applied to any individual plant (7, pp. 320-324). Yet the work on *Phormium* breeding by Yeates shows that over thirty varieties have a basic chromosome number of 16, and that chromosome behavior is regular (57, p. 112). Cockayne also reported the presence of polymorphic hybrids when *P. tenax* grows in company with *P. colensoi* (8, p. 127). Consequently the two "easily recognizable species" of *Phormium* may not have validity in the modern taxonomical conception. Hence Atkinson states "the classification is for the sake of convenience" and "it should be clearly understood that such an arrangement is to a large extent
artificial" (2, p. 206). However Hooker (18, p. 287) states that because these two species seem "to be permanently distinct, as they differ in distribution somewhat, and so much in appearance as to be universally distinguished, I have thought it better to retain them as distinct".

The plants used for this study are considered to be Phormium tenax Forster. Their characteristics conform very closely to the descriptions of the species which appear in Hooker's "Handbook of the New Zealand Flora" (18, pp. 286-287), and Cheeseman's "Manual of the New Zealand Flora" (7, pp. 320-324).

In New Zealand, wild Phormium is commonly found in association with Cordyline australis, Typha angustifolia, Calystegia sepium, and a few species of Carex, Rubus, and Festuca (9, p. 174). The plants occur in a wide range of soil and topography, and grow in various habitats - swamp, rocky, loose stone, and sand dune areas (8, pp. 62-416). Reports from South Africa and other countries show that the plants grow very well with annual rainfalls of from 20 to 150 inches, and from sea level to 4000 feet. However, a maritime condition is preferable and they cannot tolerate temperature under 9°F. (2, p. 203; 26, pp. 194-195). In New Zealand the wild Phormium is in bloom from about November to January (2, p. 209), but it blooms from May to August in southern Oregon.
The cultivation of *Phormium tenax* has long been established in many countries and studies on the plant have been reported periodically. The literature is very extensive and scattered, and most of the reports are concerned primarily with its agricultural aspects (2, pp. 283-289; 9, pp. 172-184; 10, pp. 190-195), chemical nature of the leaf and its gum (1, pp. 226-228; 37, pp. 161-162), and also on the structure and size of the leaf fibers (14, p. 278; 17, pp. 99-100; 25, pp. 370-371; 33, pp. 121-130; 53, p. 980). Literature concerning the anatomical aspects of the plant is quite limited, and the relatively few studies were concerned primarily with gross morphology.

The first investigation of the structure of *P. tenax* was probably that of Hutton in 1869 (24, pp. 111-116) who was concerned primarily with the gross structure of the mature leaf. Atkinson (2, pp. 212-215) and Gehlsen (15, pp. 193-194) also described the structure of the plant, with the most extensive study being that of Atkinson in 1921. However, these works are again concerned chiefly with the gross morphology of the plant and the internal structure of the mature leaf.

Since the leaf fiber of the plant is commercially important the structure and size of the individual fiber
has been investigated from time to time (38, p. 422).
The reported measurements of the individual fibers are
extremely variable, probably due to differences resulting
from sampling, from variation in age of leaf when samples
were taken, and from variations in locality where the
plants were grown.

The work presented here is concerned with the origin,
development and structure of the vegetative parts of the
plant and the development of the megagametophyte.
MATERIALS AND METHODS

Most of the materials for this study were collected directly from the field in a well established experimental planting of the U.S.D.A. near Goldbeach, Oregon, at an elevation of only a few feet above sea level.

Some plants were removed from the field, planted in large pots and placed in the greenhouses of Oregon State College, Corvallis, Oregon. These were used primarily as a source of root tips and for a study of the origin and development of adventitious and lateral roots.

Phormium tenax has a very short, upright shoot springing directly from the rather large rhizome, or rootstock, which gives off stout, fleshy, adventitious roots varying from a few inches to several feet in length. These roots mostly spread in a horizontal direction near the surface, but some of the roots penetrate deeply into the soil. The equitant leaves on each branch are arranged in the form of a fan which usually consists of about eight or more leaves with the youngest one in the center and the oldest at the outside. The leaves are very thick and coriaceous, tough, flexible, 3 to 6 feet long or more, 2 to 5 inches broad, linear-ensiform, rigid at the base, erect, rather dull green above, somewhat silvery and glaucous below. Each leaf is folded along the midrib with the upper surface innermost, while on the outermost surface the midrib forms
a sharp keel along the back of the leaf. The midrib and margin are bordered with a red or orange line. The tip of the leaf is always slit when mature.

The flower-stalk grows out from the center of the fan, which dies after fruits are matured. The life of the particular shoot ends with its production of fruit, but the rootstock sends forth branches which develop into new flowering shoots. The stout stalk varies from 5 to 15 feet in height, is reddish purple in color, and often more or less glaucous with wax. The dull-red flowers are numerous on the upper scapes and the branches of the flower stalk are in a two-ranked arrangement. The flower buds are protected by large bracts which fall off at the time the flower opens, or sometimes several days later. The flowers are usually 1 to 2.5 inches long with the six perianth segments connate in the lower part and nearly straight or lightly recurved at the tip. Six stamens are inserted at the base of the segments to form two whorls of three each. The filaments of the outer whorl are considerably longer than those of the inner one. The superior, tricarpellary ovary possesses a simple style which is usually about the same length as the filaments of the inner whorl of stamens.

The fruit is a loculicidal capsule which varies in length from 4 to 8 inches, is erect or inclined, stout, and never twisted. At maturity it splits into three
segments, each of which contains numerous shining black, flattened seeds.

Collections of ovaries in various stages of development were made on June 12, 1956. The nature of the inflorescence makes it possible to collect all stages from very young flower buds to open flowers at one time.

Leaves were collected at various times but most of this study is based on the leaf samples collected September 12, 1956 from plants about 5 years old.

Stem tips were collected on August 18, 1957 and April 5, 1958 from 3- to 4-year old plants. To insure proper killing and fixing of the apex, all except two or three of the leaves which ensheath the apex were excised.

Stems or upright root-stocks were collected on June 12, 1956 from 5-year old plants and samples were taken at and near the base of the stem. Additional materials were collected on August 18, 1957 from 3-year old plants and samples were taken from the apex to the base of the stem.

Adventitious roots were collected at various times from plants in the field and from potted plants in the greenhouses. Root tips approximately equal in size were fixed in the same vial to reduce the effects of the fixing agent to a constant. The most suitable size for handling, fixing, preparing and observing is a tip 0.5 to 1.0 mm. in diameter. Root materials for the study of the origin
and differentiation of primary tissues were collected on September 12, 1956 and August 18, 1957. The materials were collected from roots which were 10 to 14 inches long and variable in diameter. Samples were taken from the tip to the base of the root at intervals of 2 to 3 inches.

Flower-stalk samples were collected on June 12, 1956 from 5-year old plants.

Leaf, root, stem, and flower-stalk materials were killed and fixed in either 50 per cent formalin-aceto-alcohol or in Randolph's solution (28, pp. 41-45). The formalin-aceto-alcohol gave better results and was used exclusively for the later collections. Stem tips, root tips, and ovaries were killed and fixed in Navashin's fixing solution, Graf III (45, p. 18) which gave excellent results for all these materials. A low vacuum was used either in the field or in the laboratory immediately after collection, and the materials were left in the killing solution over night. All materials fixed in Navashin's or Randolph's solution were washed in running water for at least two hours but not over four hours, and those fixed in formalin-aceto-alcohol were washed in 50 per cent alcohol by making 4 changes in 12 hours. Dehydration and infiltration were accomplished by using the tertiary butyl alcohol-paraffin oil schedule recommended by Johansen (28, pp. 130-132). Leaf samples were subsequently embedded in
Tissuemat with a melting point of $56^\circ -58^\circ C.$, while all other materials were embedded in Tissuemat with a melting point of $54^\circ -56^\circ C.$.

Paraffin blocks containing the embedded materials were usually soaked in water at $38^\circ C.$ for several days before sectioning. Samples of older leaves could be sectioned only after the paraffin blocks were cut to expose the material and soaked at the same temperature for 45 to 60 days in a solution composed of Dreft 4 g., glycerol 40 c.c., and distilled water 360 c.c. (40, pp. 115-118). Serial cross and longitudinal sections of both root tips and leaves were cut 10 to 15 microns in thickness, young ovaries at 8 microns, and more mature ovaries at 12 to 15 microns. Sections were stained for the most part with safranin, anilin blue, and Harris's haematoxylin as recommended by Popham et al. (42, pp. 185-190). Sections of ovaries were stained with safranin and fast green.

Leaf samples were macerated in Jeffrey's solution, which is composed of equal parts of 10 per cent aqueous nitric acid and 10 per cent aqueous chromic acid (28, p. 104). The fiber cells separated in about 36 hours after which they were washed thoroughly with water, and stained with 1 per cent safranin for about 6 hours. They were then dehydrated by passing them through several changes of a mixture of one part absolute ethyl and one part tertiary butyl alcohol, and then into pure tertiary butyl
alcohol. The fibers were then cleared in xylol and mounted in a synthetic resin.

All photomicrographs were made with 4x5 Kodak Panatomic-X film. All drawings of megagametophyte development were made with the aid of a camera lucida and are reproduced at a magnification of 830 X.
OBSERVATIONS

**Origin of adventitious roots**

There are a great number of investigations on the origin and development of adventitious roots in monocotyledons but exact knowledge of their origin and early organization is still limited. Mangin (35, pp. 216-353) studied the development of adventitious roots in a number of monocotyledons and stated that the adventitious roots arise from the net-forming layer "Couche dictyogene", except for the root cap which develops from the stem cortex. Mann (36, p. 217) concluded that in the garlic the young root appeared to arise from a group of dividing cells which were near to or perhaps a part of the net-forming layer. Krauss (29, pp. 551-553), in her extensive work on morphology and anatomy of pineapple, stated that the adventitious root was initiated in the region of the meristematic ring just external to the procambial strands at the periphery of the stele.

In this report, the term "primary thickening meristem" of Esau (12, p. 377) is preferred instead of "net-forming layer" or "meristematic ring" of other authors.

The adventitious root of Phormium tenax is endogenous in origin, and as it emerges from the stem it generally passes through the sheathing bases of the leaves. The
adventitious root is initiated in the vicinity of the primary thickening meristem which is the layer of meristematic cells between the cortex and central cylinder of the stem. At the point where the adventitious root arises, the primary thickening ring becomes very active and divides repeatedly in all planes to form a domelike mass of cells (fig. 1). Subsequently several layers of stem cortex adjacent to the region of root initiation becomes meristematic and gives rise to the rootcap cells. The cells of the endodermis at the tip of the dome inside the developing root cap divide periclinally to give rise to the initial cells of the root cortex, and the cortex of the adventitious root is soon formed (fig. 2,3). A definite apical meristem is clearly evident by this time, and further development of tissues within the adventitious root results from the activity of established histogens. The endodermis of the adventitious root is continuous with the endodermis of the stem (fig. 4). The vascular elements of the adventitious root which differentiate from the root apex eventually anastomose with the vascular elements of the stem. The adventitious root then penetrates obliquely downward through the parenchymatous tissue of the stem cortex and the sheathing bases of the leaves. It is clearly evident, from the examination of the fresh material, that the cortical cells of the stem immediately in front of the adventitious root tip become
softer than elsewhere in the cortex. This indicates that digestive action takes place because of enzymes secreted by the developing root. The cortical cells in the area along the length of the root are crushed but they leave only a small amount of debris of collapsed cell walls since they appear to have been mostly dissolved by enzymatic action.

Ontogeny of the root

Perhaps the earliest work on the organization of the root tip is that of Nageli in 1845 (40, pp. 138-210). He proposed the apical cell theory which states that all the cells of the root have their genesis in a single apical cell. Probably no important advance along this line was made until 1868 when Hanstein (cited by Schmidt 47, pp. 380-388) developed the classical histogen theory which was accepted by various botanists and still is of great service in the interpretation of the apical meristem, especially of the root. The histogen theory as applied to roots emphasizes that the main body of the root arises not from a superficial cell but from a several-layered meristem at a considerable depth in the root tip. These meristemmatic areas which give rise to specific regions of the root were called histogens. The histogens are the dermatogen which gives rise to the primodial epidermis,
the periblem which gives rise to the cortex, the plerome which forms the stele, and the calyptrogen which produces the rootcap.

Janezewski (27, pp. 162-201), Treub (cited by Schade et al. 46, 170-173), and Flahaout (13, pp. 1-168) classified root apices of monocotyledons into three types based upon the histogen theory. The first type embraces the rare cases in which the initials of the histogens, calyptrogen, dermatogen, periblem and plerome, are independent. The second is characterized by three groups of initials. The calyptogen and plerome have separate initials, while the periblem and dermatogen are derived from a common group of initials. The root apex of this type is typical of plants in Gramineae. The third type has only two groups of initials, one giving rise to the plerome and the other to rootcap, dermatogen and periblem. This type appears very commonly among the plants in Liliaceae.

Treub (cited by Schade et al. 45, pp. 170-173) also described another minor type which is transitional between the second and third types.

In all Phormium tenax roots investigated the apex consists of six cytomorphological zones distinguished by the arrangement of cells and the staining reactions of the cytoplasm. They are the plerome, the periblem, the dermatogen, the calyptrogen, the columella, and the peripheral part of the rootcap. Three sets of initials
can be recognized in the root apex at the meristematic region (fig. 5, 27). The plerome initials, a small group of about 5 to 8 meristematic cells at the tip of the plerome, give rise to the entire vascular cylinder. These initial cells are more irregularly arranged than are the other histogen initials. The small group of 3 to 6 cells just beyond the plerome initials gives rise to two distinct dermal layers, the dermatogen and the cortical layers. The calyptrogen initial cells are just ahead of the dermatogen-periblem initials and by periclinal divisions they give rise to the columella. The peripheral part of the rootcap is also derived from the calyptrogen initial cells by both anticlinal and periclinal division as well as divisions in oblique planes.

The cells of the rootcap are roughly isodiametric. The external elements are elongated in the direction of the root axis, whereas the internal elements of the columella tend to be elongated at right angles to the root axis. The cells of the columella are usually rather regularly arranged, large, and hexagonal in shape. They form longitudinal files of cells from the calyptrogen down to the tip of the rootcap. All the cells are parenchymatous, contain large nuclei and a considerable amount of starch granules, but the peripheral cells that are not alive contain no starch granules and their cell walls probably contain mucilagenous substances.
Just above the initials the cells making up the immature cortex are compact and devoid of intercellular space. There are about five layers of cells in the periblem at this level. However the number of cell layers is gradually increased in the older portions of the root by periclinal as well as anticlinal divisions of the young cortical cells. Periclinal divisions were observed to occur more abundantly in the inner layers surrounding the differentiating central cylinder. These two or three layers of cells stain more intensely and have a dense protoplasmic content (fig. 5). At the level of about 21 microns above the initial region, the cortex is more distinctly differentiated from the central cylinder. The cortical cells become larger, more vacuolated, and small intercellular spaces develop throughout the cortex. The cells of the central cylinder are smaller, have denser cytoplasm, and intercellular spaces do not develop. The innermost layer of the cortex adjacent to the pericycle appears as a distinct layer which consists of tightly packed cells which are elongated longitudinally and tangentially but are narrow in a radial direction. This layer of thin-walled cells is considered as the young endodermis. The Casparian strips in the endodermal cells are first noticeable at a level just above the root hair zone (fig. 10,11). The cells just beneath the epidermis form a rather definite uniserate layer which probably give
rise to the thick-walled cells of the several-layered hypodermis in the mature portion of the root. The cell walls of the endodermis, hypodermis, and also the inner layer of cortical cells just outside the endodermis thicken gradually as the cells mature. Thus the endodermis becomes a single layer of thick-walled cells when the root tissues are fully developed, while the hypodermis consists of several layers of thick-walled cells with the outermost layer composed of cells in which the outer tangential walls are the thickest (fig. 13,14). The cells of the inner cortical layer just outside the endodermis become thickened on their radial, transverse and inner tangential walls and appear U-shaped in transverse section (fig. 13).

The dermatogen is composed of a single layer of cells which at first are somewhat elongated radially (fig. 5), and in which all cell divisions are anticlinal. The cells have a prominent nucleus and dense cytoplasm in the meristematic region of the root tip. At a level just above the root-hair region, or about 2 cm, above the initials of the root, most of the epidermal cells lose their cell contents, gradually collapse and are finally sloughed from the older portions of the root.

Immediately above the initials region of the central cylinder the cells of the stele begin to differentiate the various primary tissues. The outermost continuous layer
of the stele becomes distinguishable by its compact uniform arrangement of cells (fig. 6). This develops into the pericycle which thus originates as a unicellular layer. As the central cylinder develops further, however, the pericycle undergoes a series of anticlinal as well as periclinal divisions and becomes a multiseriate layer which varies from 2 to 4 cells in thickness in older portions of the root (fig. 13). The interior cells of the young central cylinder divide in all planes but especially longitudinally. As a result the central cylinder increases in diameter up to the level where the protophloem mother cells become mature. The number of protoxylem ridges and primary phloem strands that differentiate varies with the size of the root and ranges from 5 in the smaller roots to 25 in the larger ones.

Protophloem first becomes distinguishable as isolated phloem mother cells approximately 180 microns above the root initials (fig. 7). The first protophloem cell in each radial row is usually diamond-shaped in cross section and is located just beneath the uniserate pericycle layer. The cell walls of protophloem cells stain darker than the walls of adjacent cells, yet their protoplasm stains conspicuously lighter than in other surrounding cells. The primary phloem strands appear to mature at approximately 130 microns above the initial appearance of the protophloem mother cells (fig. 8). The nuclei disappear
and the protoplasm is reduced to a thin layer in each cell as the protophloem sieve-tube elements undergo elongation. Companion cells are not present in protophloem but the metaphloem sieve-tube elements are accompanied by companion cells. The metaphloem differentiates in a centripetal direction with respect to the protophloem. Phloem parenchyma is lacking, which is a common characteristic of the phloem of many monocotyledonous plants.

About 50 microns above the root initials, immature metaxylem vessels are distinguishable in the central cylinder by their oval shape, and their size which is considerably larger than that of the adjacent cells (fig. 6). They take up stain lightly at this time probably due to degenerated protoplasm and high water content as pointed out by William (55, p. 458). The protoxylem elements, though they become completely differentiated before the metaxylem cells (11, p. 490) are not distinguishable at this level. At a level of about 480 microns above the root initials, the protoxylem elements can be recognized and appear in alternation with the radial rows of protophloem. The first protoxylem vessels differentiate adjacent to the uniseriate pericycle. They are somewhat oval in cross-section and considerably narrower in diameter than the developing metaxylem. The protoxylem reaches maturity at about 1.5 cm. above the initials region while the metaxylem cells are still undergoing vacuolation and enlargement.
Thus maturation of the primary xylem also occurs in the centripetal direction. The mature protoxylem elements have annular or spiral secondary wall thickenings. The first metaxylem vessels reach maturity at about 7 cm. above the initials region. The secondary walls of these first metaxylem vessels are usually scalariform. The later formed vessels will differentiate reticulate or pitted secondary walls. The metaxylem vessels have simple perforation plates on their more or less oblique to transverse end walls. At about 9 cm. above the initials all the metaxylem is mature.

A cross-section of a large mature root (fig. 12) shows numerous radial plates of primary xylem and primary phloem in the stele. The protoxylem vessels are smaller and usually have thicker cell walls than the metaxylem vessels. The groups of primary phloem which alternate with the xylem groups consist of sieve tubes with companion cells. They are separated from the groups of xylem by a few rows of parenchymatous cells which gradually develop thickened cell walls. The center of the central cylinder is occupied by thin-walled cells, some of which contain a resin-like substance which is probably the same as the gum exuded from the leaves. This substance is precipitated by alcohol and was identified as a polyceronide by McIlroy (37, pp. 161-162).
The pericycle is composed of several layers of cells in which the cell walls become considerably thickened. The continuity of the pericycle is sometimes interrupted opposite the protoxylem ridges. Passage cells are also evident in the endodermal layer. They are represented by thin walled cells, whereas thickening occurs on all the walls of the other endodermal cells (fig. 13). The cortex of mature root is composed of many layers of thin-walled parenchymatous cells with many large intercellular spaces scattered throughout. Thus the parenchymatous cells of the cortex are easily crushed (fig. 12).

Origin of lateral roots

Lateral roots are initiated in the pericyclic region of the parent root (fig. 15). William (55, pp. 455-456) recently reported that initiation of lateral roots occurs in the meristematic root tip of several monocotyledons but in this study the first evidence of root initiation has been seen only in the region just above the root-hair zone. A group of pericycle cells located opposite one of the protoxylem ridges becomes meristematic. As a result of subsequent periclinal and anticlinal divisions of the pericycle cells the endodermis of the parent root becomes stretched, the cells divide periclinally for a few divisions and then rupture. The pericycle cells give rise
to all tissues of the embryonic lateral root (fig. 16,17). Janezewski (27, pp. 162-201) states that the pericycle cells of the parent root in seed plants give rise only to the central cylinder of lateral root, while the endodermis and one or two adjacent cortical parenchyma cell layers of the parent root give rise to the cortex, epidermis, and cap of the lateral root. Popham (43, pp. 269-272) also considered that lateral root formation in Pisum sativum involves a few layers of cortical parenchyma lying close to the endodermis. He considered that these cortical parenchyma cells participate in the formation of the primordial rootcap. However, the interpretation of the early organization of the lateral root in this study seems to agree with the work of Van Tieghen et al. (54, pp. 611-660) who stated that all tissues derived from the endodermis and cortical parenchyma are not a part of the lateral root but form a 'digestive' pouch only.

The meristematic cells originating from the pericycle gradually become transformed and differentiated into a definite root-cap, apical meristem, and histogens similar to those of the parent root. Vascular elements of the lateral root connect with the vascular elements of several of the xylem and phloem strands in the parent root (fig. 18). The embryonic lateral root then forces its way through the digested cortical tissue and hypodermis of the parent root.
The vegetative shoot apex

The structure and mode of growth of the shoot apex in species from the major groups of plants has been described by many investigators. Several different theories have been used recently to describe the structure and mode of growth of the angiosperm shoot apex but the basic concept is probably that of Schmidt's tunica-corpus theory (47, pp. 350-390). From his work on the shoot apex in many species from ten different families, he did not agree with the unrealistic zonal pattern suggested by Hanstein in 1868 (cited by Schmidt 47, pp. 380-388).

Gifford (15, pp. 477-529), in a modern review of the shoot apex of plants, stated that the original concept of the tunica-corpus theory is that "the tunica consists of a layer or layers of cells in which divisions are predominately anticlinal. The corpus represents another initiation zone in which cell divisions occur in various planes." However, many reports on the division pattern of the tunica layer or layers during the past twenty years do not conform with the description of the tunica mentioned above (44, pp. 28-69; 48, p. 778; 49, pp. 245-282; 50, pp. 276-277). Many workers (3, pp. 820-832; 5, pp. 656-664; 22, pp. 404-411) have described zones in the angiosperm shoot apex which are distinguished not only by direction of cell division but also by cell size,
nuclear size, rate and plane of cell division, density of cell contents, reaction to plasma and nuclear stains, thickness of cell wall and polarity of growth.

The vegetative apex of *Phormium tenax* is elevated at the tip of the upright root-stock and is covered by numerous leaves. The shoot apex is in the form of a spherical dome about 90 to 120 microns high and 150 to 175 microns broad above the latest formed leaf primordium (fig. 19). In transverse section, the outline is more or less circular (fig. 20).

The interpretation of the shoot organization is probably best described by the modified tunica-corpus theory which has been used effectively by Stant for many monocotyledons (51, pp. 115-129; 52, pp. 441-448). The meristem is differentiated into the two distinct zones of tunica and corpus. The corpus is differentiated into three more or less distinct zones, the rib meristem, the flank meristem, and a group of corpus initial cells (fig. 28).

The tunica consists of two layers (fig. 19). In the outermost layer there is evidence only of anticlinal divisions and the layer would thus appear to remain discrete throughout the ontogeny of the vegetative shoot. The second tunica layer divides only by anticlinal divisions at the summit of the apical mass but on the flank above the point of leaf initiation, occasional periclinal
divisions occur. The corpus, the initial mass of cells bounded by the tunica layers, consists of densely staining dividing cells which divide by both periclinal and anticlinal divisions as well as obliquely. In the region below the summit of the tunica there is a group of large, vacuolated cells which serves as the corpus initials. The corpus initial cells, by anticlinal divisions, give rise to the rib meristem and the flank meristem. The rib meristem, the central region of the corpus in which divisions are predominantly anticlinal, consists of vacuolated dividing cells. The cells are usually regular in orientation and arrangement but they may become irregular where occasional periclinal divisions occur. The cells of the rib meristem form a rather uniform column to a considerable depth in the root-stock. The flank meristem, the peripheral region of the corpus, consists of slightly elongated cells which are the result of both periclinal and anticlinal divisions.

Anatomical structure of stem

The stem of *Phormium tenax* is an upright root-stock which is for the most part underground. Externally, the nodal and internodal regions are difficult to distinguish because the internodes are very short. The stem is round in transverse section, and the older portions are covered with the remnants of dead, sheathing leaf bases.
Internally the stem is differentiated into two distinct zones, a central core which consists of scattered collateral bundles and ground parenchyma, and a thick layer of thin-walled parenchyma cells. A distinct endodermis separates the two zones. For the sake of convenience in describing the internal structure and its development, the central core of scattered bundles will be referred to as the central cylinder, and cortex will be used for the parenchyma tissue outside the cylinder as has been done in other investigations of monocotyledonous stems (30, pp. 170-175).

At the stem apex and beneath the bases of the several youngest leaves surrounding the apex is a region of rather uniform parenchymatous tissue with conspicuous procambial strands extending into the developing leaves. Below this region there are two to three layers of rather uniformly arranged cells which form a distinct meristematic layer, the primary thickening ring. This primary thickening ring, established about 0.1 mm. from the shoot apex, separates the central cylinder from the cortex. Starch grains are more abundant in the cells of this zone than in the rest of the ground tissue of the stem (fig. 23). The meristematic ring, which forms a hollow cylinder between central cylinder and cortex, is interrupted frequently by leaf traces which leave breaks in the meristematic ring similar to leaf gaps. These are not exactly
comparable with leaf gaps in dicotyledonous stems, however, since typical leaf gaps are in vascular tissue.

This meristematic ring is considered to be a specialized meristem which Mangin (34, pp. 216-363) called the "Couche dictyogene". It produces inwardly the procambial strands, which develop into the scattered vascular bundles, and the parenchyma in which they are dispersed. Increase in diameter of the stem is the result of the activities of this meristematic layer, and also by the general division and expansion of cells of the ground tissue. Some procambial strands are differentiated entirely with this narrow zone of the meristematic ring to form a vascular network at the periphery of the central cylinder. The outer portion of the layer produces some cells of the cortex and finally the endodermis. The meristematic ring is also responsible for the initiation of the adventitious roots as mentioned before. As the vascular tissue in the network which separates the cortex and central cylinder mature, meristematic activity is reduced in the meristematic ring and finally ceases. Thus the boundary between the central cylinder and the cortex is marked by the vascular network which is bounded externally by the endodermis. The vascular network and endodermis is, of course, interrupted by large openings through which pass the leaf traces (fig. 29).
The endodermal cells in younger portions of the stem do not differ greatly in shape and form from the cells of the ground parenchyma of the cortex and central cylinder. Gradually these cells develop well defined Casparian strips (fig. 24). Starch also disappears from cells of the endodermis. In the mature stem the inner tangential, transverse and radial walls of the endodermal cells become prominently thickened and lignified.

The vascular tissue of the central cylinder consists of two more or less separate sets of vascular bundles, the peripheral bundles and the more scattered bundles in the central portion. The peripheral bundles form a complex network that is compact in the older stem but more open near the stem apex (fig. 22, 25). The scattered bundles inside this network are common bundles which are leaf traces and branch traces. They are embedded within a mass of parenchymatous ground tissue which consists of irregularly arranged cells with thin cellulose walls and abundant starch grains. Small intercellular spaces are present throughout this mass of parenchymatous cells.

The vascular pattern in the *P. tenax* stem is considered to be a modified palm type of vascularization. That is, the course of each vascular bundle is not in a single plane, but is directed variously in oblique, horizontal and vertical planes. As the larger bundles are traced inward and downward from the leaf, each one follows
a path from the base of the leaf directly across the cortex and into the central cylinder through a gap in the peripheral vascular networks. Within the central cylinder the bundle continues to follow an obliquely downward course to approximately the center of the stem axis. It then turns outward and downward in a broad curve toward the peripheral network. The course of the bundle then become directed vertically downward for a short distance after which the lower end swings outward to unite with elements in the vascular network (fig. 29).

Each large common bundle may branch at any point along its course. These branches are directed downward until they anastomose with other bundles. This branching and anastomosing of bundles usually occurs near the center of the central cylinder. Thus in a transverse section a large, consolidated mass of vascular elements is frequently seen at the center of the stem axis. Thus, unlike many monocotyledonous plant, the anastomosing of the bundles in the stem of *P. tenax* does not occur at any specific region along the axis, and there is no evidence of an orientation of the bundles into nodal and internodal regions in the anatomical structure of central cylinder.

The smaller bundles of the leaf are branches of the large leaf traces. These branches arise at any point after a large trace leaves the central cylinder, and continue
vertically in the cortex for varying distances before entering the leaf.

The leaf traces as they enter the central cylinder are essentially collateral bundles as they are in the leaf. However, as the bundles approach the center of the central cylinder they are usually modified from collateral to an amphivasal arrangement. This is probably due partly to the twisting of the leaf-trace bundles at approximately the center of the central cylinder and partly to the anastomosing with smaller bundles. Also, the xylem shifts from the endarch condition with well-defined protoxylem to a poorly defined mesarch condition. Each amphivasal bundle consists of xylem which surrounds a very small strand of phloem.

The cortex is composed of thin-walled parenchymatous ground tissue and a distinct hypodermis of several layers just inside the epidermis. In the young portion of the stem the hypodermis is difficult to distinguish from the other cortical cells. In the mature portion of the stem it consists of several rows of cells distinct in type from those other cortical cells. The outermost row consists of thick-walled cells which are arranged in regular longitudinal rows. The outer tangential walls are extremely thick. The cells are polygonal in shape in cross section and with the larger diameter in the tangential plane. The cells in the inner rows of the hypodermis
resemble those of the outer row in shape but the walls are uniformly thick and they are not arranged in regular longitudinal rows. All the cells of the hypodermis are without starch grains.

The cortex is traversed by three types of vascular tissue. The large leaf traces pass obliquely upward and outward from the vascular network to the leaf. The smaller bundles of the leaf continue vertically upward for some distance after they leave the vascular network and before they enter the leaf. Both of these types of bundles are essentially collateral in the cortex. The vascular tissue of the adventitious root is in the form of a protostele that usually is directed obliquely downward and outward from the peripheral network of the central cylinder.

Development and structure of the leaf

The _Phormium tenax_ leaf has the same basic pattern as many other monocotyledons with equitant leaves. This type of leaf is characterized by a sheathing leaf base which is succeeded by an upper region flattened in the vertical plane, the blade, in which its anatomical structure is isobilateral. The leaf of _P. tenax_ also has this general form but in addition, between the short leaf base and the blade, there is a short vertical ensiform region where anatomical structure shows a transition between sheath and blade (fig. 30). However the very young leaves
are entirely open except at the base which forms a sheath which almost surrounds the stem apex.

The leaf primordium arises laterally from the shoot apex about 45 to 55 microns below its summit (fig. 31). A leaf primordium is usually initiated by the occurrence of a few periclinal divisions in the outer corpus. The first tunica layer over the primordium divides only anticlinally and maintains its identity throughout the period of initiation and further development of the leaf. Continued divisions of the corpus cells in both periclinal and anticlinal-oblique planes result in a perceptible swelling of the primordium which first appears as a hemi-elliptical mass of cells at the side of the shoot apex. The primordium continues to enlarge and, as a result of a rapid lateral spread of periclinal divisions in the corpus, the thumb-like protuberance is transformed into a crescent and then into an annular swelling that encircles the shoot apex. Since the leaves are in two ranks the two encircling edges of the primordium apparently overlap (fig. 32). Thus the future sheath is tubular at the extreme base but has two overlapping edges higher up.

The leaf primordium increases in length rapidly during its early development due to rapid division of the cells at the edge and also by division in all planes of the cells throughout the corpus. The tunica, of course, increases in length by anticlinal divisions only. During
this phase of growth the cells of the abaxial side divide more rapidly than those on the adaxial side and the young primordium gradually assumes a vertical position.

When the primordium attains a height of 75 to 90 microns the subapical cell is recognizable by its unique appearance. It may remain nonfunctional for a time, then undergo a periclinal division followed by an anticlinal division of the inner daughter cell. This results in an inverted "T" arrangement of cells. Thus the growth of the primordium during this time is due primarily to the activity of this subapical initial cell which divides periclinally at irregular intervals and its derivatives subsequently divide anticlinally, periclinally, and obliquely. New cells are being added to the interior in this manner as well as by the division of cells at the margins.

By the time the primordium is 120 to 150 microns in height, some of the cells in the central region undergo longitudinal divisions and the median procambial strand is differentiated. This appears first near the base of the primordium and then develops in an acropetal direction toward the primordium tip and also basipetally until it becomes associated with the procambial tissue in the stem (fig. 33). Additional procambial strands representing the lateral veins of the leaf are rapidly differentiated in the same manner.
During this early stage of leaf development the tip of the young leaf is bent inward over the shoot apex because of the unbalanced growth of the abaxial side of the young primodium. Though the subapical meristem still maintains its meristematic potentiality, the increase in height of the leaf during this stage appears to be due in part to the activity of an intercalary meristem at the base of the leaf. The subapical meristem soon loses its ability to divide and further growth and differentiation are due mostly to the intercalary meristem and the general division of cells of the parenchymatous ground tissue. However the ground tissue probably retains its meristematic potentiality for only a short time as the cells soon lose their meristematic appearance and become highly vacuolated. The cells, exclusive of those in the epidermis and procambial strand, are now subglobose in shape and small intercellular spaces are numerous.

The mature leaf is composed of four distinct fundamental tissues, the epidermis, the hypodermis, the mesophyll, and the fibrovascular tissue (fig. 36). The epidermis consists of a single layer of cells enveloping the entire surface of the leaf on both sides. It is derived by anticlinal divisions of the first tunica layer of the shoot apex. Thus it is a protective layer which is continuous with the epidermis of the stem. Periclinal divisions do not occur and the epidermis remains as a single
layer throughout the life of the leaf. There are no modified structures or appendages on the entire surface of the leaf with the exception of stomata and cuticle. The size and shape of the epidermal cells on the adaxial and abaxial sides are different. The epidermis on the adaxial side consists of cells that are arranged in uniform rows, are more rectangular in shape and elongated in the direction of the leaf axis. The walls of the cells are smooth and straight in younger leaves, but in the fully developed leaf the lateral walls become undulate. The inner wall becomes thickened in such a way that its upper surface becomes concave, and the outer wall becomes slightly convex. A heavily thickened cuticle covers both surfaces but it is very much thicker on the adaxial surface and thickest on the abaxial surface of the midrib (fig. 37). Stomata occur on both sides but are more abundant on the abaxial than on the adaxial side. The guard cells contain chloroplasts though they are lacking in the rest of the epidermal cells.

The hypodermis consists of cells which are generally similar in shape and size. They are rather elongated in the direction of the leaf axis and generally rectangular in shape. There are from one to several rows of hypodermal cells lying beneath the epidermis of the upper side of leaf only.
The mesophyll is not differentiated into palisade and spongy layers. All cells being essentially alike, they are isodiametric and nearly spherical with thin cellulose walls and numerous small intercellular spaces. This mesophyll extends from the lower epidermis to the hypodermis, interrupted only by the fibrovascular bundles and large air canals that are usually found between the bundles. Starch grains and the chloroplasts are present in all cells.

The most interesting feature of the foliage leaf of *P. tenax* is the type and distribution of the vascular bundles with the associated extraxylary fibers. The longitudinal fibrovascular bundles are conspicuous even to the unaided eye in both transverse and paradermal longitudinal sections. In fresh sections the larger bundles appear as white bands running from the lower epidermis to the hypodermis of the leaf. As is common with other monocotyledons, these fibrovascular bundles are parallel to one another through most of the leaf and gradually converge toward the tip. There are bundles of three sizes in a regular arrangement that is common in many monocotyledonous plants. The largest vascular bundles are regularly spaced across the leaf with the vascular tissue located in the center of the distance from the lower to the upper side of leaf. Smaller vascular bundles alternate regularly with the large bundles with the vascular tissue
located slightly below the middle of the leaf. The fibers of bundles of both sizes extend from the lower epidermis to the hypodermis. Still smaller bundles are frequently found between the larger and smaller bundles. The vascular tissue in these is located below the level of the other bundles, and the associated fibers extend only downward to the lower epidermis. The smallest bundles are differentiated and mature later than the larger ones during the development of the leaf (fig. 34).

The vascular bundles are of the collateral type with the xylem toward the top of the leaf and the phloem below. Extraxylary fibers are associated with all the bundles but are most abundant in the fibrovascular bundles of the two larger sizes. Thus the larger fibrovascular bundles form the conspicuous white bands seen in freshly cut sections. This is the most striking characteristic feature of the bundles in the leaf blade of F. tenax. In many other monocotyledons the fibrous sheaths occur only as caps over the xylem and under the phloem, or only under the phloem. In the young leaf, and in the basal portion of the old leaf of F. tenax, the vascular bundles also have incomplete fibrous sheaths, but as tissues differentiate within the leaf additional strands of such presclerenchyma cells are developed. The walls of young fiber cell are thin but become sclerenchymatized when mature. The ends of the sclerenchymatous fiber cells taper gradually to
points that overlap the ends of adjacent fibers. The overlapping of the ends of these fibers and the interlocking of adjacent cells are believed to contribute much toward the mechanical strength of the leaf as it matures.

The extraxylary fibers

Various authors reported on the structure and size of the individual extraxylary fiber (38, p. 422). However the reports on the length as well as the breadth of the fibers are extremely variable. This probably is due to the method of sampling as well as to environmental factors. The fibers observed in this study varied from 0.48 to 1.25 cm. in length and from 7 to 22 microns in diameter. They are approximately cylindrical in shape and the ends taper gradually to a point. The surface of the fiber cell wall is generally smooth but wavelike irregularities are not uncommon (fig. 38). The fibers are somewhat circular in cross section with uniformly thick cell walls. They have a circular or oval lumen which disappears near the end of the cell.

Megagametophyte development

The development of the megagametophyte in seed plants has been of considerable interest with regard to ontogeny, and especially because of phylogenetic implications. A
voluminous literature related to these problems has been devoted to many species of seed plants (34, pp. 84-145). Wunderlich (56, pp. 437-502), in his comparative embryological and anatomical studies on the Agavaceae, reported some embryological characteristics of several genera in the family, but Phormium was not included. Cave (6, p. 144) reported that P. tenax has 16 pairs of chromosomes with no great differences between them. With regard to the megagametophyte, she states that "the antipodals are well developed, and strikingly different from those in the other genera of the tribe, giving the impression of synergid cells with pointed tips".

At the time of the differentiation of integuments, a single hypodermal archesporial cell is produced in the ovule. This archesporial cell functions directly as the megaspore mother cell (fig. 39). It becomes somewhat more prominent than the rest of the cells of the nucellus by its larger, centrally located nucleus. The epidermal cells of nucellus divide to form additional cells between megaspore mother cell and epidermis (fig. 40). Cell divisions continue throughout the ovule and a massive nucellus is developed. Meanwhile the integuments are differentiated and develop to cover and surround the nucellus more or less completely by the time the megaspore mother cell is ready to undergo meiosis. The ovule by this time is anatropous.
The very large nucleus is usually located toward the micropylar end of the elongated megaspore mother cell at the zygotene stage (fig. 40). The megaspore mother cell continues to elongate throughout the first meiotic division. At diakinesis there are 16 pairs of chromosomes that are approximately equal in size (fig. 41). This agrees with the count reported by Yeates (57, p. 112) and Cave (6, p. 144). The first division of the megaspore mother cell results in the formation of two cells which are approximately equal in size (fig. 42, 43). These divide immediately at approximately the same time (fig. 44) and form a group of four megaspores arranged as a linear tetrad. The cell toward the chalazal end of the ovule is considerably longer than the other cells of the tetrad (fig. 45, 46). The three outer megaspores begin to degenerate, the cytoplasm becomes densely granular, chromatin clumps in the nuclei, and the cell walls collapse. Thus it is usually the innermost megaspore that becomes the functional one (fig. 47, 48).

The functional megaspore enlarges rapidly and its nucleus undergoes three successive mitotic divisions. The primary micropylar and antipodal nuclei derived from the first mitotic division of the megaspore (fig. 49) migrate to the micropylar and the chalazal end, respectively, of the developing gametophyte (fig. 50). Numerous small vacuoles appear in the cytoplasm of the developing
megagametophyte, and frequently large ones appear in the center. Then a large vacuole develops between the two nuclei and increases in size until it occupies the central portion of the 2-nucleate embryo sac (fig. 50, 51). These nuclei then undergo the second mitotic divisions which occur simultaneously to form the 4-nucleate stage (fig. 52). At this time there are two daughter nuclei at each end of the enlarged megagametophyte, separated by a large central vacuole. The nuclei then divide simultaneously by the third mitotic division to form 8 nuclei (fig. 53). These are arranged as a micropylar and chalazal quartet separated by the central vacuole. There is a considerable increase in the amount of cytoplasm in the cell during these later divisions.

Shortly after the megagametophyte reaches the 8-nucleate stage, one nucleus from each quartet migrates toward the center of the cell. The nucleus from the micropylar end of the megagametophyte seems to move up very rapidly while the one moving down from the chalazal quartet moves very slowly or not at all. Thus the two polar nuclei approach each other in the vicinity of the chalazal end of the megagametophyte, remain in contact for a short time, and then gradual fuse prior to fertilization. During this time membranes are laid down around each of the other six nuclei by cell-plate formation to establish three cells at each end of the embryo sac, and separated
by the central proendosperm cell that contains the fused polar nuclei (fig. 54, 55). The three antipodal cells differentiate before the egg apparatus. The antipodal cells here are ephemeral and will degenerate shortly after fertilization.

The synergids, which are located side by side at the tip of the micropylar end of the gametophyte, assume a pyriform appearance and develop a faintly staining filiform apparatus. A large vacuole usually appears in each synergid in the basal portion of the cell. These synergids begin to degenerate soon (fig. 56) and the cell walls may collapse before fertilization.

The egg cell meanwhile enlarges and develops a large vacuole in the micropylar end of the cell. The egg is pear-shape and is situated partially between the synergids. Only the chalazal part of the egg cell extends into the space between the free ends of the synergids. The nucleus is located in this chalazal end of the egg cell, and is fertilized in this position.

Thus the megagametophyte of *P. tenax* follows the 'Polygonum' type of development (34, pp. 87-97). At maturity a dense cytoplasmic strand extends from the egg apparatus to the chalazal end of the cell. The large polar nucleus is suspended in this central strand (fig. 56).
The adventitious roots of *P. tenax* originate in the vicinity of the meristematic ring of the stem. The endodermis and a few layers of the cortex of the stem are also involved in the formation of the tissues of the adventitious root. The central cylinder containing the vascular tissues of the root arises from a small group of initials in the tip of the plerome, while another small group of meristematic cells just beyond the plerome gives rise to the cortex and epidermis. The rootcap is derived from the calyptrogen initials. The pattern of primary vascular tissue differentiation resembles, in general, that found in other monocotyledons. The initial differentiation of xylem occurs centrifugally and acropetally, preceding phloem differentiation, but maturation of sieve tube elements occurs before maturation of xylem elements. Lateral roots originate from the pericycle just above the root-hair zone. Subsequent differentiation is similar to that which occurs in adventitious roots.

The meristem of the vegetative stem apex of *P. tenax* is differentiated into distinct tissue zones of tunica, corpus initials, flank and rib meristem. The tunica consists of one or two layers and there is no evidence of periclinal divisions in the outermost layer.
The young shoot has a well-defined cortex and vascular cylinder separated by the primary thickening meristem. The primary thickening meristem gives rise to the provascular strands and vascular network that constitutes the periphery of the central cylinder. The leaf traces in the stem are arranged according to the palm type of vascularization. Anastomoses of the traces connect only to the external surface of the vascular network. The endodermal cells show well-defined Casparian strips and lignified walls. The endodermis of the stem is continuous with the endodermis of the adventitious root.

The leaf primordia arise laterally from the shoot apex by periclinal divisions of the outer cells of the corpus. During early development, the primordium increases in length by divisions of the ground parenchyma cells and also by the activity of a subapical cell. As the leaf gets older continued growth and differentiation is the result of the activity of an intercalary meristem at the base of the leaf.

The mature blade is composed of four distinct fundamental tissues: the epidermis, a hypodermis just beneath the upper epidermis, the mesophyll, and the fibrovascular tissue. Though there is a cambium-like zone in the young vascular bundle, only primary tissues are present in the collateral bundle of the leaf. The fibrous bundle sheaths
of the larger bundles extend from the xylem to the hypodermal layer and from the phloem to the lower epidermis.

Individual fibers from a leaf about 4 years old are long, tapered, thick-walled cells which vary in length from 0.48 to 1.25 cm. and in diameter from 7 to 22 microns.

The megaspore mother cell is formed directly from a single hypodermal archesporial cell. The chalazal megaspore of the linear-tetrad functions to give rise to the 8-nucleate 'Polygonum' type of embryo sac in the usual way.

At diakinesis of the megaspore mother cell there are 16 pairs of chromosomes that are approximately equal in size.
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Figure 1-4. Transverse sections of the stem showing the development of adventitious roots. Fig. 1. Early appearance of the adventitious root. X 200. Fig. 2-3. Further development; Fig. 2. X 100, Fig. 3. X 200. Fig. 4. The endodermis of stem continuous with the endodermis of the adventitious root. X 200. B, cortex of stem; C, cortex of adventitious root; D, root-cap; E, endodermis; F, initiating point of adventitious root; VN, vascular network of stem.
Figure 5. Median longisection of the root tip; CL, central cylinder; CO, cortex; E, epidermis; ICL, initial of central cylinder; IC, initial of cortex and epidermis; IRC, initial of root-cap. X 150.

Figure 6-8. Cross sections of the root at 50, 180, and 310 microns, respectively, above the root initials. Fig. 6. Early differentiation of the pericycle (P) and immature metaxylem vessels (A); CO, cortex. X 200. Fig. 7. Early differentiation of the protophloem (B). X 200. Fig. 8. Mature protophloem (B) sieve tube. X 200.
Figure 9. Transverse section of root at the root-hair zone; A, protoxylem; B, protophloem; C, cortex. X 100.

Figure 10. Endodermis with casparian strip (E). X 100.

Figure 11. Enlargement of a portion of Fig. 10; E, endodermis; P, pericycle; C, cortex. X 400.

Figure 12. Mature root; E, thick-walled endodermis; D, pith cell with latex substances. X 50.

Figure 13. Enlargement of a portion of Fig. 12; A, protoxylem elements; B, protophloem elements; P, pericycle; E, endodermis with passage cell (C). X 400.

Figure 14. Enlargement of portion of Fig. 12; H, thick-walled hypodermis; EP, thin-walled epidermis. X 400.
Figure 15-18. Transverse section of the adventitious root showing the development of lateral root; E, endodermis; C0, cortex of parent root; C, cortex of lateral root. Fig. 15-16. Initiation of lateral root in the pericycle. X 300. Fig. 17. The lateral root just prior to time of differentiation of root apex initials. X 100. Fig. 18. The vascular connection of the lateral root. X 100.
Figure 19. Median longitudinal section of the vegetative shoot apex. X 200.

Figure 20-21. Transverse sections of a portion of the young vegetative stem approximately 24 and 84 microns, respectively, below the summit of the shoot apex. A, shoot apex; B, C, D, E, first, second, third, and fourth leaf respectively. X 100.

Figure 22. Transverse section of stem about 0.6 mm below shoot apex. M, meristematic ring; CC, central cylinder; CO, cortex. X 100.
Figure 23-25. Further maturation of stem. Fig. 23. Transverse section of stem about 1.4 cm. below shoot apex. M, meristematic ring with abundant starch grains in the cells; CC, central cylinder; CO, cortex. X 200. Fig. 24. Transverse section of stem older than the one in Fig. 23. E, endodermis with casparian strips; VN, vascular network. X 600. Fig. 25. Transverse section of mature stem. T, mature meristematic ring forming a thick layer; CC, central cylinder; CO, cortex. X 200.

Figure 26. Transverse section of old flower-stalk, showing the resemblance of its structure to the stem. X 100.
Figure 27. Diagramatic drawing of root tip. CL, central cylinder; CO, cortex; E, epidermis; ICL, the initials of central cylinder; IC, the initials of cortex and epidermis; IRC, the initials of root-cap; C, column; RC, root-cap.

Figure 28. Diagramatic drawing of shoot apex. T, tunica; C, corpus; CI, corpus initials; FM, flank meristem; RM, rib meristem.

Figure 29. Diagram of the course of vascular bundles in stem. AD, adventitious root; LG, leaf gap; VB, leaf trace bundle; VN, vascular network.
Figure 30. Diagram of plant; five older leaves were cut off at sheathing base region.

The youngest leaf (left) is open to the base, the next older one (right) has an open sheath at A, a concrescent region at B, and a flat blade at C. In the vascular bundles the xylem is shown in black and the phloem is white.
Figure 31-33. Early development of leaf. Fig. 31. Longitudinal section of stem tip. A, leaf primordium; B, procambium strand in young leaf. X 400. Fig. 32. Transverse section just below base of apical meristem. A, B, C, first, second, and third leaf, respectively; D, procambium of median vascular bundle; E, procambium of lateral vascular bundle; M, stem tip. X 200. Fig. 33. Longitudinal section of shoot apex. B, D, procambium strands in first and fourth leaf, respectively. X 100.

Figure 34. Transverse section through intercalary region of a leaf sheath. F, immature fiber cells; VN, transverse branch passing from one longitudinal vascular bundle to another. X 100.
Figure 35-37. Structure of leaf. Fig. 35. Cross section of immature vascular bundle. C, cambium-like zone; X, xylem; P, phloem; F, fiber cells, X 200. Fig. 36. Cross section of mature leaf. A, parenchymatous cells surrounding the vascular bundles; B, hypodermis; E, upper epidermis with thick cuticle; F, fiber cells, X 100. Fig. 37. Cross section of median bundle. F, fiber cells; VN, mature vascular bundle, X 100.

Figure 38. Fiber cells, X 400.
Figure 39-51. Development of the megagametophyte. The micropylar end of the developing gametophyte is directed downward in all figures. X 830.

Figure 39. Ovule with archesporial cell.

Figure 40. Ovule with megaspore mother cell at zygotene.

Figure 41. Diakinesis in megaspore mother cell.

Figure 42. Metaphase of first meiotic division.

Figure 43. Dyad.

Figure 44. Metaphase of second meiotic divisions.

Figure 45. Telophase of second meiotic divisions.

Figure 46. Linear tetrad of megaspores.

Figure 47. Functional and three degenerating megaspores.

Figure 48. Functional and degenerating megaspores.

Figure 49. First mitotic division of functional megaspore.

Figure 50. Early 2-nucleate stage.

Figure 51. Late 2-nucleate stage.
Figure 52-56. Development of the megagametophyte (continued).

Figure 52. 4-nucleate stage.
Figure 53. 8-nucleate stage.
Figure 54. Early seven-celled, 8-nucleate megagametophyte.
Figure 55. Fusion of the two polar nuclei.
Figure 56. Mature megagametophyte.