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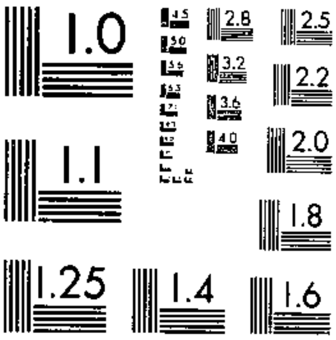

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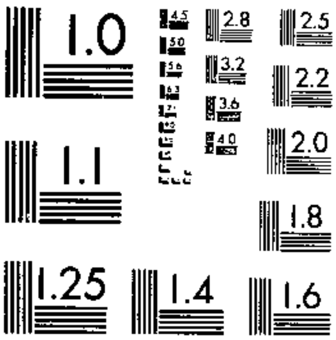

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Contribution to the Morphology and Anatomy of Guayule (Parthenium argentatum)[1]

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CONTENTS

INTRODUCTION

The researches of Ross (*5*)[3] and Lloyd (*4*) have shown that rubber storage in guayule is a function of the living parenchyma cell of root and stem. In plants of harvest size these cells are limited largely to the vascular rays and the cells around the secondary resin canals, whereas in young material the primary cortex and pith are of greater importance.

Although rubber secretion is a physiological function of the cell that may differ in intensity in different plants and under different environmental conditions, performance is evidently bound up with structure; that is, a plant with a greater storage capacity, one that has a broader secondary cortex and wider and more numerous vascular rays, should outyield a plant in which the anatomical picture reveals a preponderance of mechanical tissue.

Three decades of breeding work at Salinas, Calif., have produced varieties that outperform indigenous plants both in total yield and in

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[2] Credit is due to Mrs. Eugenia Artschwager for preparation of the drawings, and to R. A. Laubengayer, Cornell University, for embedding certain guayule material in celloidin and preparing slides of some of it.

[3] Italic numbers in parentheses refer to Literature Cited, p. 33.

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percentage of rubber. Individuals of these high-yielding strains, if their anatomy were known, should have a broad secondary cortex and a minimum amount of sclerenchymatous tissue; the vascular rays of the xylem would be broad and numerous; they would grow rapidly in the spring, producing a favorable balance of phloem tissue and synthesize a maximum amount of rubber within the shortest time interval between seasons of growth. One might further project that such plants would not be too choosy in regard to soil requirements and could be fitted profitably into existing systems of crop rotation.

Unfortunately, aside from conspicuous grosser morphological differences, little is known about the distinguishing anatomical characteristics of high- and low-yielding varieties, still less about the effect of environment on structure, and nothing at all about the cause of reversion from high rubber content to low when put in a different environment.

Rapid growth and intensity of rubber storage are mutually exclusive unless a suitable rest period is allowed for rubber synthesis to be effective. Rapid growth, although producing a larger total increment of both xylem and phloem, favors xylem development unless growth is suspended by the withholding of irrigation water after a maximum amount of phloem has been formed. Plants differ not only in their ability to produce a relative growth increment of xylem and phloem but also in regard to differentiation priority between the two tissues. In many plants the cambium differentiates a certain amount of phloem first when growth is resumed in the spring, and guayule appears to be one of them, although our knowledge concerning this point is mostly empirical.

Ross (5) and Lloyd (4), through their studies, have given us a general insight into the anatomy of the plant, the ontogeny of the tissues, and the place and time for rubber synthesis, but they tell us very little about the detailed structure of the secondary xylem and phloem, so important in the development of the plant from the standpoint of performance.

This bulletin aims to consider critically and briefly the plant in its entirety, laying emphasis on structural features that have been previously neglected or omitted and that, in the author's opinion, have a direct bearing on breeding to serve the present need.

MATERIALS AND METHODS

Most of the material for study came from the United States Cotton Field Station at State College, N. Mex., having been imported a decade ago from various parts of the Big Bend area of Texas, with some from Salinas, Calif. The usual technique of fixing and staining was employed but often had to be abandoned in favor of hand sections of fresh material. Old stem and root material treated with hydrofluoric acid and embedded in celloidin proved useless for the study of the secondary phloem, but untreated, dissected secondary phloem embedded in hard paraffin and stained with iron alum haematoxylin showed fine differentiation even though, on account of the large amount of sclerenchyma, the sections were somewhat ragged. Maceration of the xylem for a study of its components was carried out in a mixture of 10 percent chromic acid and 10 percent nitric acid.

Instead of alkannin, Sudan III was used for the staining of rubber. By making the sections fairly thick and washing thoroughly in alcohol after staining, it was possible to remove from the section all rubber that might accidentally have been dragged with the knife into adjacent cells. Such a preparation counterstained with chloroiodide of zinc showed, in addition to rubber, the location of starch to best advantage.

All photographs were taken on Wratten M plates with suitable liquid filters. The drawings are mostly based on photomicrographs.

FIGURE 1.—Average growth habit of guayule. (Photographed by A. R. Leding.)

GROSS MORPHOLOGY

Parthenium argentatum Gray, a member of the tribe Heliantheae, family Compositae, is a profusely branching shrub attaining an average height of somewhat less than 2 feet (fig. 1).

The root system (fig. 2), like that of many other desert shrubs, consists of a taproot that penetrates deep into the subsoil and a system of shallow laterals that extends horizontally for long distances and whose fibrous tertiary rootlets cover with their fine net the very surface of the soil, utilizing even the shallow moisture of short, sporadic rains.

The young stem is silvery gray and densely clothed with hairs. As the epidermis is shed and cork and lenticels develop, the surface becomes gray, later brownish; it is generally fissured with shallow, sometimes deep corky cracks, and parts may be covered with deposits of resin oozing out from the peripheral canals.

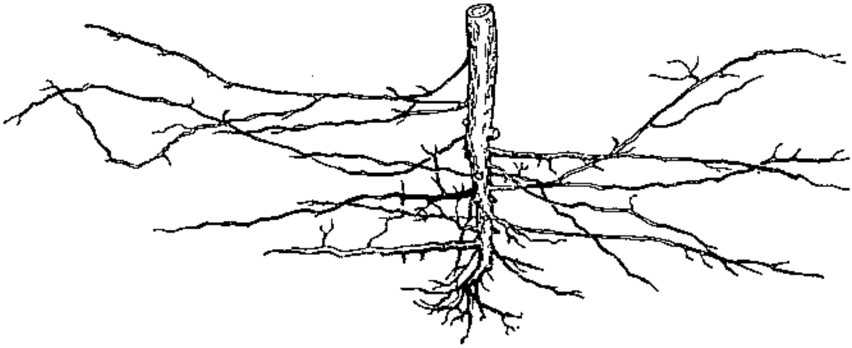


FIGURE 2.—Surface root system of young plant.

The leaves are inserted on the stem in a spiral with a divergence of 2/5. However, opposite and even whorled arrangements may be found on the same stem. The leaves are lanceolate, usually crenately toothed, or cut-lobed below the middle and densely covered with asymmetrical T-shaped hairs; the leaf form is very variable. During the winter months only the terminal leaf clusters are retained; these leaves are smaller than the summer leaves, lanceolate, and rarely lobed.

The inflorescence (pl. 1, *A*) is a compound, one-sided cyme with lateral axes exceeding the main axis in length.

MORPHOLOGY OF FLOWERS AND SEED

The morphology of the flowers of guayule and the related species, *Parthenium hysterophorus* L., has been treated in great detail by Kokieva (*3*), and a similar detailed treatise by Dianova and coworkers (*2*) furnishes a comparative cytoembryological analysis of *P. argentatum* Gray and *P. incanum* Gray.

The flowers of guayule are borne in close heads on a common receptacle. The heads are rarely solitary; commonly a number of them are grouped close together (pl. 1, *A*) and, since they are not initiated simultaneously, flowering extends over a long period.

Each flower head consists of 5 involucral leaves (fig. 3, *B*) that overlap slightly at the base. Above the involucral leaves and alternating with them are 5 bracts containing in their axils the 5 ligulate or ray flowers (fig. 3, *A*, *E*). Adnate to each ligulate flower are 2 disk flowers enclosed in saclike bracts (fig. 3, *F*, and fig. 4, *A*). The remaining surface of the disk is filled with disk flowers and their bracts (fig. 3, *A*). The bracts of the ligulate flowers are almost round and their surface is densely covered with hairs. Those of the disk flowers are membranaceous scales with infolded margins (fig. 3, *D*), also densely pubescent, and each with a solitary vascular

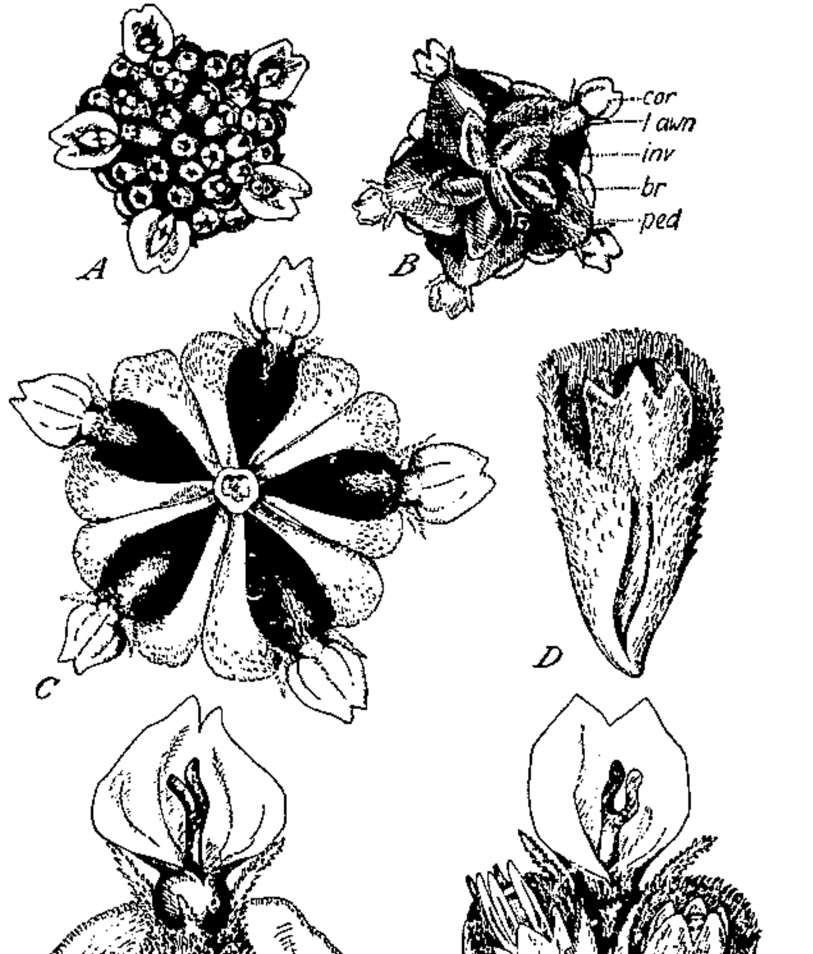
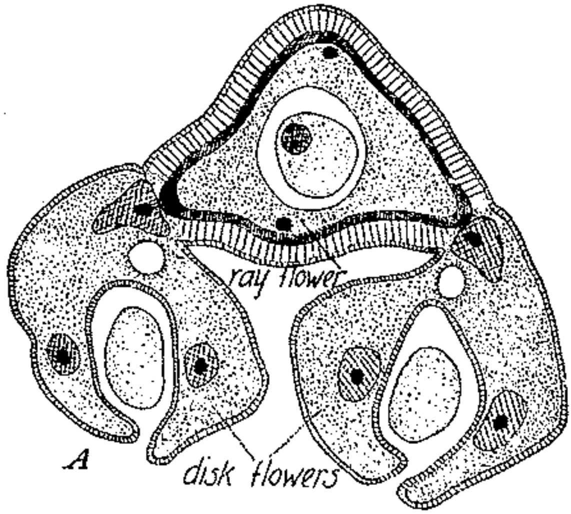


FIGURE 3.—*A*, Surface view of flower head showing 5 ligulate and 24 disk flowers. *B*, Rear view of flower head; *cor*, lobe of corolla; *l. awn*, lateral awn; *inv*, involucral leaf; *br*, bract of ray flower; *ped*, pedicel. *C*, Enlarged rear view of mature head with involucral bracts removed to show outlines of achenes, sterile flowers attached to them, ray corollas, and pappus. *D*, Disk flower with its enclosing bract. *E*, Enlarged view of ray flower and its bract without its disk flowers. *F*, Ray flower with its 2 adnate disk flowers.



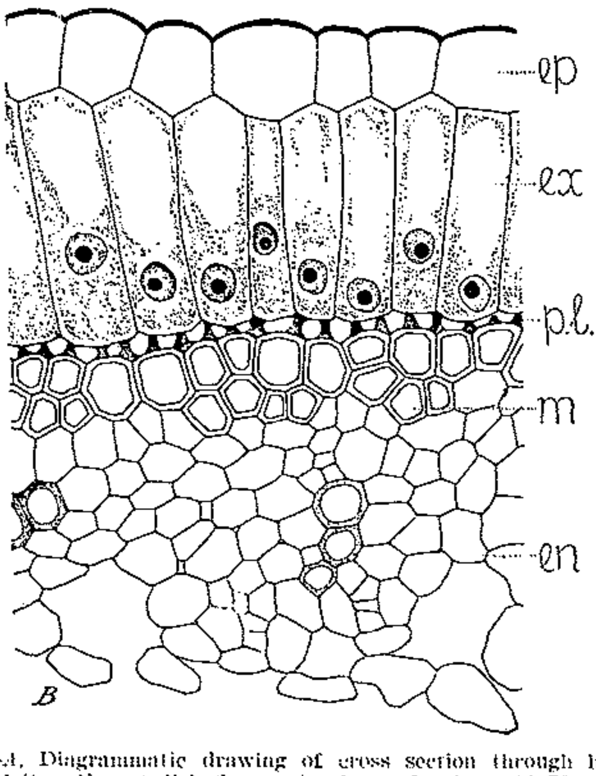
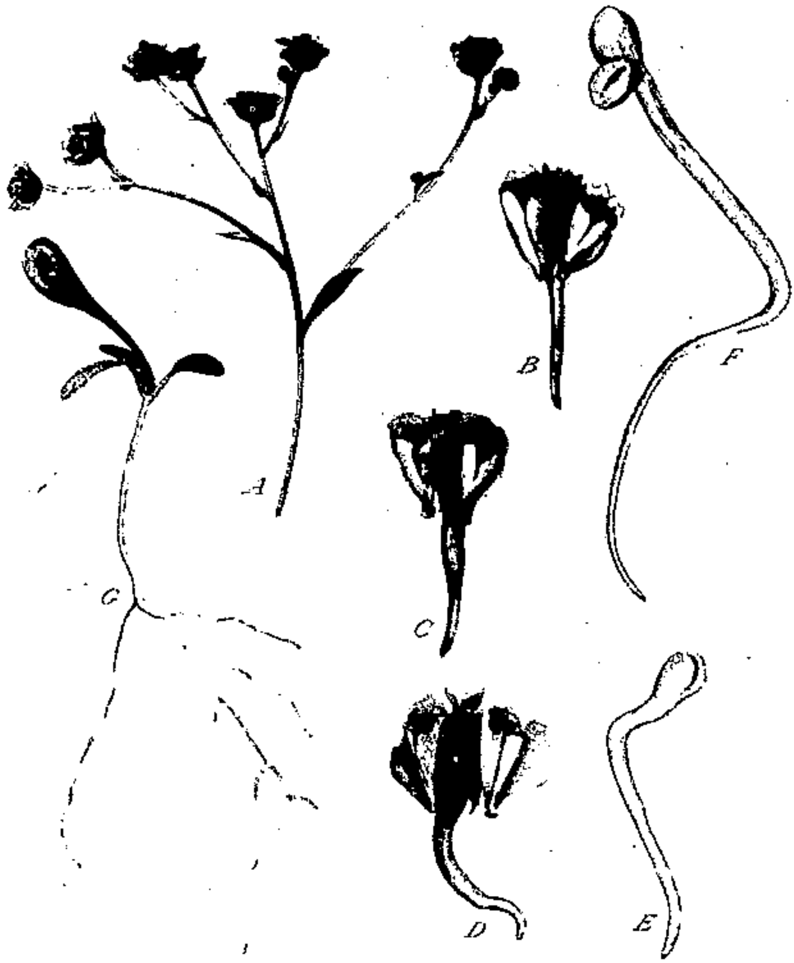


FIGURE 4.—A, Diagrammatic drawing of cross section through base of ray flower and its adjacent disk flowers to show adnation. × 52. *B*, Detailed drawing of mature ovary wall. × 750. *ep*, Epidermis; *ex*, exodermis; *p. l.*, pigmented layer; *m*, mesocarp; *en*, endocarp.



A, Branch of inflorescence with flowers in various stages of development; B–D, germinating seed; E–F, young seedlings; G, older seedling.

A, Young seedlings showing root, hypocotyl, and one pair of foliage leaves. *B*, Seedling axis at junction of hypocotyl and root; just below bulge the first lateral root makes its appearance.

bundle. The bracts of the 10 disk flowers that are adnate to the ray flowers (fig. 3, *F*) are saclike and have 3 vascular bundles each.

The corolla of the ray flower is sharply cleft in front (fig. 3, *F*), entire, or slightly cleft in the rear. The corolla of the disk flower is five-lobed, and its five vascular bundles terminate between the teeth of the corolla tube.

The pistil of the ray flower is formed by two carpels grown together in the upper region to form a short style that terminates in two stigmatic lobes of equal height (fig. 3, *E*, *F*). The style is traversed by two bundles; its outside is covered by a thick, velvety pubescence. The ovule is anatropous, ovate, and flattened tangentially.

The ovary wall (fig. 4, *B*) has a single-layered outer epidermis that abuts on a row of tall palisade cells. A layer of small, thick-walled fibers composes the mesocarp. Between the mesocarp and palisade cells is a small-celled pigmented layer characterized by radial papillae and yellow content that later turns brown. The endocarp is made up of loose, irregular parenchyma cells. There are four vascular bundles traversing the ovary wall, those passing through the keels and those running through the center of the anterior and posterior walls.

The nectary forms a short tube that clasps the style, almost adhering to the outer wall. The pappus (fig. 3, *E*) consists of a short ventral and two lateral awns, densely pubescent and with a solitary vascular bundle.

The disk flowers have five stamens grown together to form a short tube that is adnate to the corolla for about half the length. Each filament has one vascular bundle. The pistil of the disk flower lacks an ovary cavity. It is at first shorter than the stamens but elongates when the flower matures, pushing up the pollen in the process.

When the fruit is ripe the flower heads disintegrate; the ray flowers that bear the seed remain attached to their adjacent disk flowers and their involucral bracts and fall away as a whole. The remaining disk flowers also drop off, leaving behind the five involucral bracts attached to the receptacle.

The actual fruit is an achene with a dry, indehiscent pericarp, shrivelled corolla, and three short awns. The achene itself is obovate and tangentially flattened, dark gray or almost black, and covered with short hairs.

SEEDLING STRUCTURE

General Morphology

Guayule seed, unless specially treated, is slow and difficult to germinate. The root pushes out of the seed coat (pl. 1, *B*, *C*, *D*) about 6 days after planting, and the cotyledons appear above ground about 3 days later.

The young seedling has a long taproot, a short hypocotyl, and oval or orbicular cotyledons (pl. 2, *A*). The base of the hypocotyl is indicated by an abrupt increase in diameter (pl. 2, *B*) and the appearance of the first lateral rootlet below the bulge.

ANATOMY

ROOT

The taproot of the young seedling has a central core of vascular tissue (fig. 5, *A*) limited on the outside by an endodermis and a cortex.

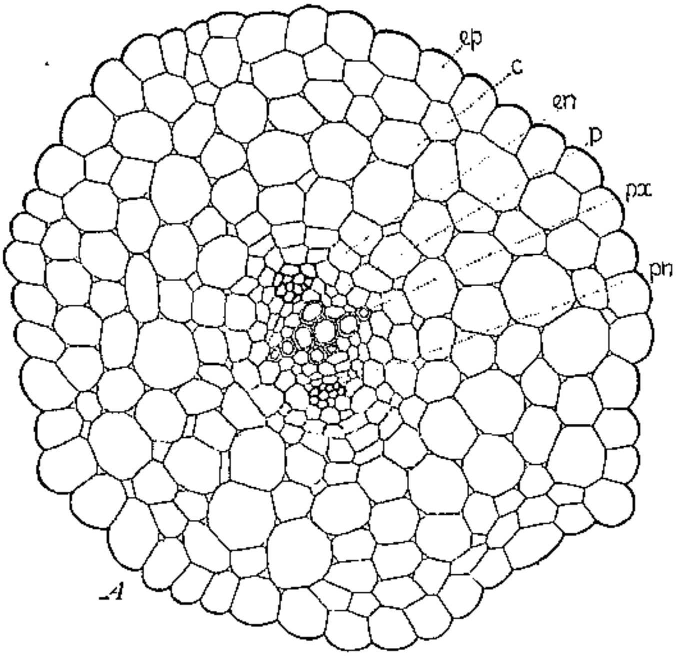
The peripheral cells of the cortex are covered by a root epidermis, a single layer of small, thin-walled cells, many of them elongated into root hairs (the latter are not shown in drawing). The cortex is five- to six-layered; its cells are large and possess prominent intercellular spaces. The stele consists of two protoxylem points extending centrifugally to the pericycle, differing in that respect from lateral rootlets that are commonly triarch (fig. 5, *B*). Between the two protoxylem points two groups of primary phloem are located, and between xylem and phloem is a mass of undifferentiated parenchymatous tissue that eventually matures into metaxylem (fig. 6). The transformation of this tissue into metaxylem proceeds in all directions except for a single layer centrad to the phloem groups which functions as a cambium, with the derived cells maturing as secondary xylem or phloem. From these points of initial cambium activity there is a progressive development with the zone of cambium extending laterally until it reaches the points where the protoxylem cells abut on the pericycle.

As the rootlet enlarges, the epidermis breaks down and its cells become lignified. The cells of the cortex enlarge and radial divisions become increasingly noticeable among them. The endodermis also compensates for stelar enlargement, first through increase in size whereby the radial walls extend from the Casparian strips outward and later by cell increase through anticlinal divisions.

In the region opposite the two primary phloem groups the endodermis becomes two-layered, but no Casparian strips develop in the upper cells. The development of this localized double endodermis is the first step in the formation of the resin canals.

The ontogeny of these canals follows a pattern common to the Compositae; the cells of the double endodermis divide anticlinally, giving rise to groups of four cells. The walls at the point where the four cells meet pull away; an intercellular space forms which gradually enlarges to form the resin canal (pl. 3, *A*). Sometimes the anticlinal divisions in the double endodermis extend only through the outer layer of cells, in which case the canal is bounded by only three cells. Subsequent periclinal divisions cut off two tiers of cells (pl. 3, *B*), the inner one known as the secreting layer or epithelium.

In somewhat older rootlets two small groups of fiber may be seen centrad to the endodermis and opposite the resin canals (pl. 3, *B*). They usually surround and crush the protophloem in their development. Although these groups of fibers often adjoin the endodermis, they also may be located several layers inward (fig. 7). Their origin is pericyclic, although Lloyd does not believe that the pericycle is involved in their formation.



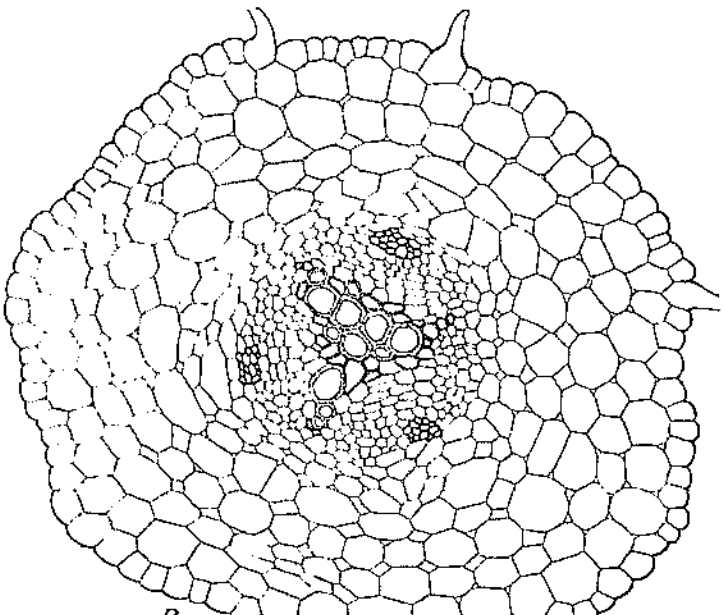


FIGURE 5.—*A*, Cross section of taproot of young seedling with diarch protoxylem plate. × 250. *ep*, Epidermis; *c*, cortex; *en*, endodermis; *p*, pericycle; *px*, protoxylem; *ph*, primary phloem. *B*, Cross section of triarch rootlet. × 250.

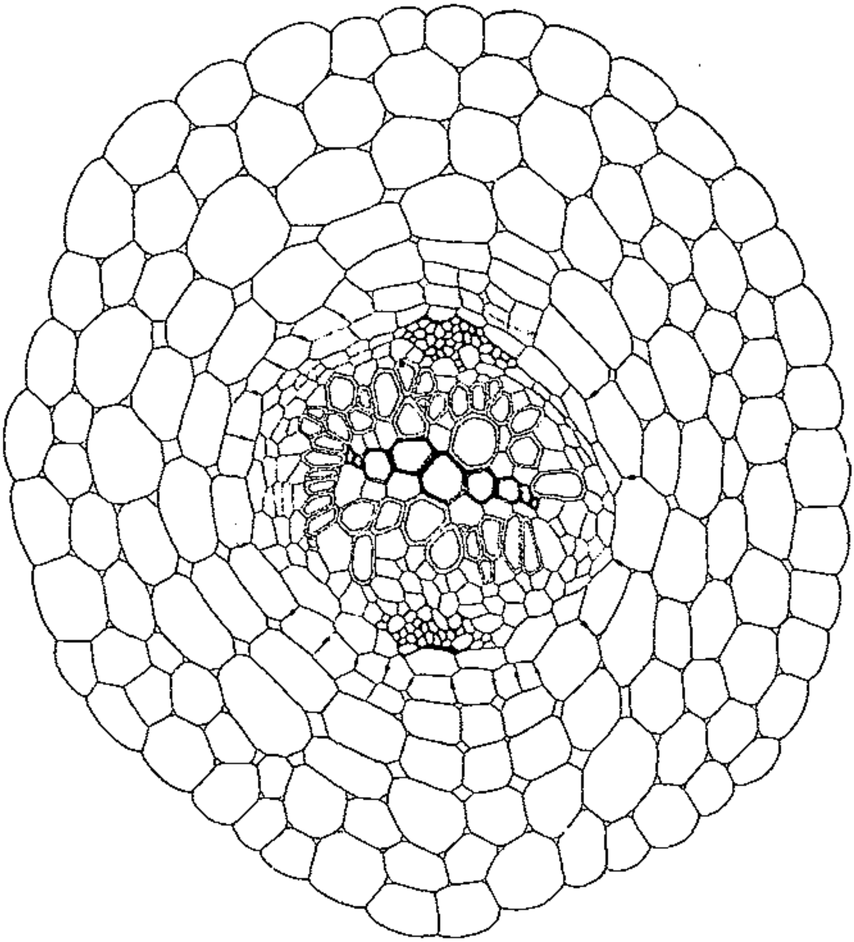


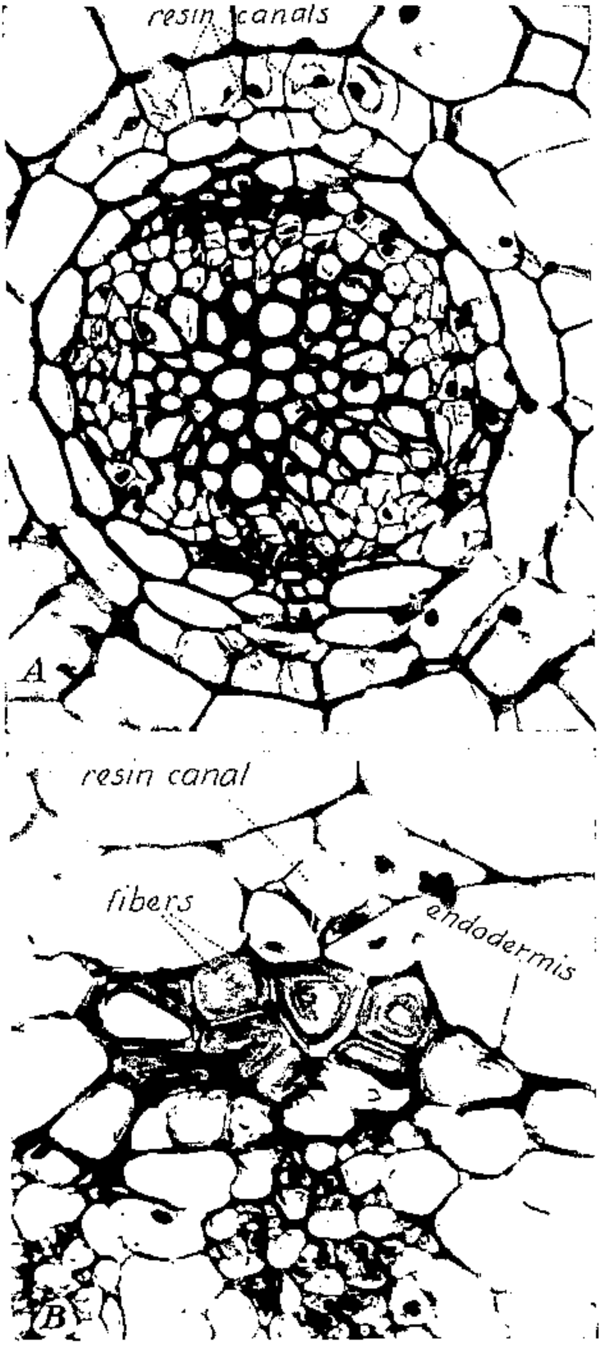
FIGURE 6.—Cross section of taproot of seedling somewhat older than represented in figure 5, *A*. The fundamental parenchyma has differentiated into metaxylem; some secondary xylem also has been added. × 560.

HYPOCOTYL

The base of the hypocotyl is rootlike, with a primary diarch protoxylem plate and laterally placed phloem groups. The cortex is broader than in the root, but there is no increase in diameter of the stele (pl. 2, *B*).

Vascular transition takes place in the hypocotyl, but the stelar tissue is not completely collateral and endarch until approximately the lower third of the cotyledonary midrib is reached. The transition agrees in general plan with *Arctium minus* Bernh., as described by Siler (*6*). The change from the exarch condition in the root to the endarch condition in the stem begins in the middle or lower part of the hypocotyl, and the complete endarch condition for the midrib bundles is attained some distance up the cotyledons, as previously stated.

Near the middle of the hypocotyl new xylem differentiates laterally to form two tangentially exarch bundles (pl. 4, *A*). The protoxylem



A, Cross section of young root showing endodermal origin of resin canals. × 240. B, Partial cross section of older root with primary cortical canal and group of pericyclic fibers above group of crushed primary phloem. × 650.

A, Cross section of upper hypocotyl of very young seedling showing two flat, V-shaped midrib bundles and two lateral traces of the cotyledons. × 470. *B*, Cross section through lower hypocotyl of older seedling showing four bundles (from these four bundles—compare fig. 8—the leaf traces of cotyledons and the first foliage leaves are derived). × 100.

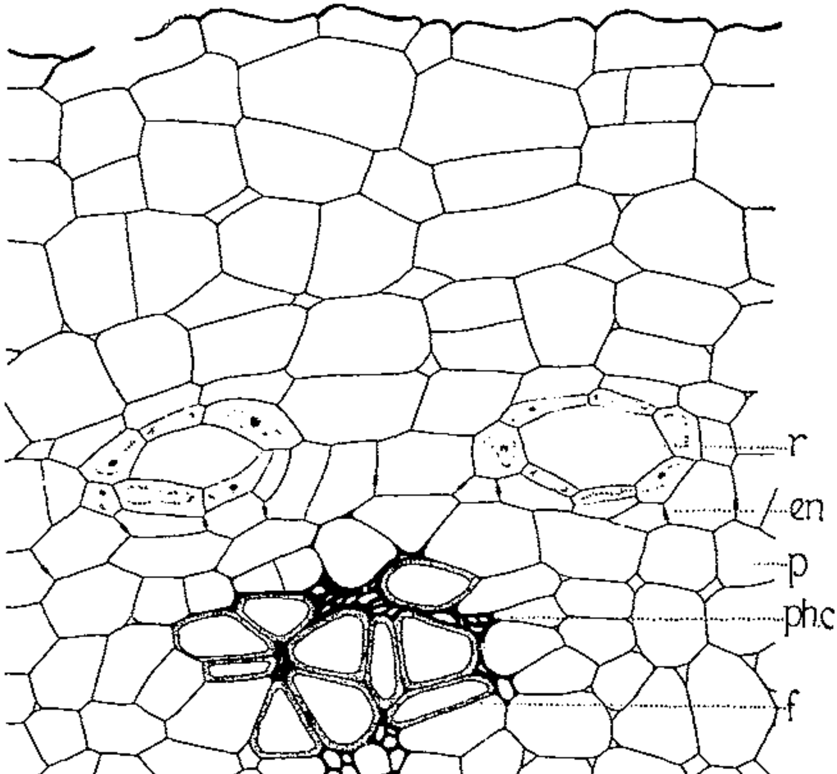


FIGURE 7.—Partial cross section of taproot 1.35 mm. in diameter, showing resin canals and group of fibers. × 410. *r*, Resin canal; *en*, endodermis; *p*, pericycle; *ph. c*, crushed primary phloem; *f*, group of primary fibers; *ph*, primary phloem; *c*, cambium; *x*, xylem.

points shift progressively centrad and become several cell layers removed from the endodermis where they eventually form flat, V-shaped double bundles. The lateral orientation of newly formed xylem elements coincides with the tangential stretching of the two primary phloem groups and their splitting to form four phloem regions, which come to lie opposite the xylem of the V-shaped bundles. These bundles of the middle and upper hypocotyl anastomose according to a definite pattern to form the vascular supply of the cotyledons and the true foliage leaves.

In very young seedlings with embryonic cotyledons, the origin and course of the vascular supply is easily followed. The V-shaped double bundles become the midrib bundles of the two cotyledons, while the lateral traces arise some distance downward. These lateral traces run separately for a considerable distance before they split to supply two lateral bundles to each cotyledon. The laterals, unlike the V-shaped double bundles of the midrib, are always endarch and, since the strands lignify basipetally in very young material, an independent development from that of the root pole is suggested by Siler (*6*) for *Arctium*. However, it appears that in guayule the two lateral traces split off from the median trace (the V-shaped double bundles) near the base of the hypocotyl, a condition which, according to Dangeard (*1*), holds true for the Compositae in general.

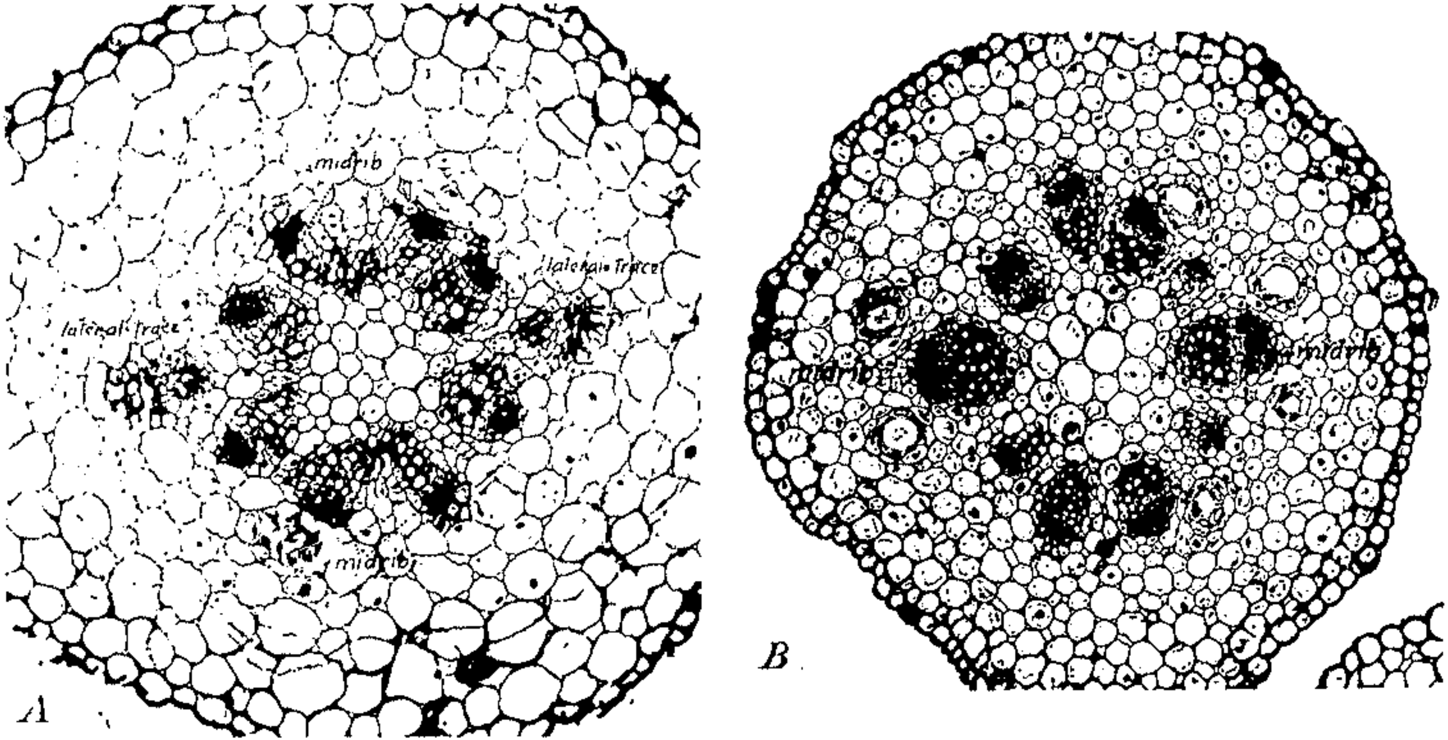
The four bundles of the lower hypocotyl (pl. 4, *B*, and fig. 10) will be designated, for convenience, as A, B, C, and D. About halfway up the hypocotyl these four bundles widen and then split to form eight bundles: A and Aa, B and Ba; C and Ca; D and Da. (See fig. 11, *A*, *B*.) From here on, the course of the cotyledonary traces and of the traces of the epicotyl that supply the first two foliage leaves may follow one of several patterns.

PATTERN I (fig. 10, *A*).—Following the differentiation of the eight strands, bundles Aa and Ca widen and give off bundles Ab and Cb and then move out into the cortex where they divide to form the lateral traces of the cotyledons (pl. 5, *A*). Bundles Ab and Cb fork again, splitting off bundles Ac and Cc; at the same time bundles Ba and Da widen and split off bundles Bb and Db. Bundles Bb and Cb fuse to form the midrib of the first foliage leaf, while bundles Ac and Db unite to form the midrib of the second leaf. The two laterals of the first foliage leaf are formed by bundles Da and Ab, whereas the laterals of the second leaf are formed by bundles Ba and Cc (pl. 5, *B*).

PATTERN II (fig. 10, *B*).—This pattern differs from the previous one in that bundles Ac and Ab as well as Cb and Cc are given off from A and C directly instead of from the two laterals Aa and Ca.

PATTERN III (fig. 10, *C*).—According to this scheme bundles A, B, C, and D split off 2 bundles each, so that a cross section taken a little below the cotyledonary node shows 12 bundles with the undivided 2 laterals Da and Ba already out in the cortex. The midribs of the first 2 leaves are fusion bundles, as in the other 2 patterns.

Lloyd's account of the course and derivation of the leaf traces (*4*) is fundamentally at variance with any of these patterns. Since his conception of the origin of the laterals differs from that of Dangeard (*1*), with whom this author concurs, a certain disagreement is to be expected.



A, Section through cotyledonary collar of young seedling. First periderm cells in outer cortex. × 144. B, Section through base of epicotyl of young seedling. The epicotyledonary midribs are flanked by two resin canals each, whereas the lateral traces of the first leaf are accompanied by one canal. × 144.

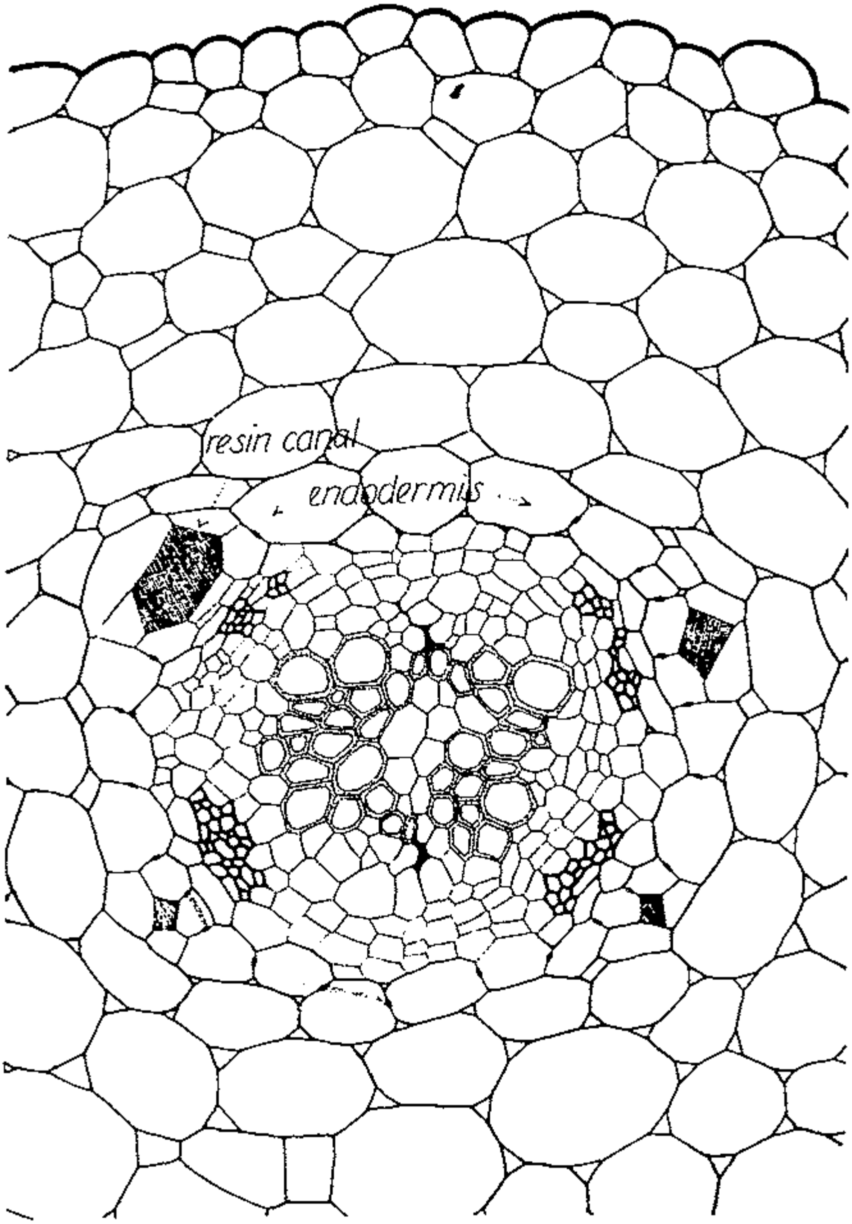


FIGURE 8.—Cross section through lower hypocotyl showing resin canals opposite the four phloem groups. The protoxylem points are several cell layers centrad from the pericycle. × 470.

The primary resin canals and fibers in the hypocotyl arise in the same manner as in the root. There are commonly four resin canals in the lower transition region, one opposite each phloem group (fig. 8). The groups of primary fibers, also four in number, usually adjoin the endodermis (pl. 3, *B*). Lloyd's own illustration (*4*) shows the fibers next to the endodermis, so that it is difficult to understand why he argues against their pericyclic origin.

Periderm is initiated in the second layer of the cortex or even more centrad (pl. 5, *A*).

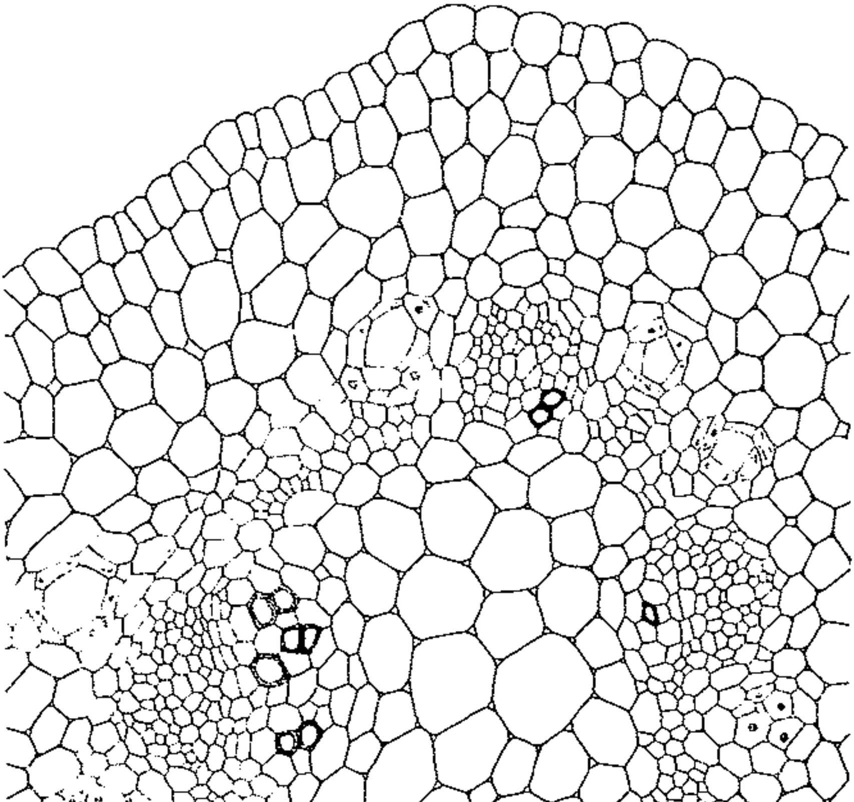


FIGURE 9.—Cross section through apical region of epicotyl showing differentiation of leaf traces and resin canals. × 365. Note that there are no resin canals in the pith.

EPICOTYL

Tissue differentiation in the upper epicotyl is illustrated in figure 9. The cortex is from four to five layers thick and is not separated from the stele by a definite endodermis. There are present eight resin

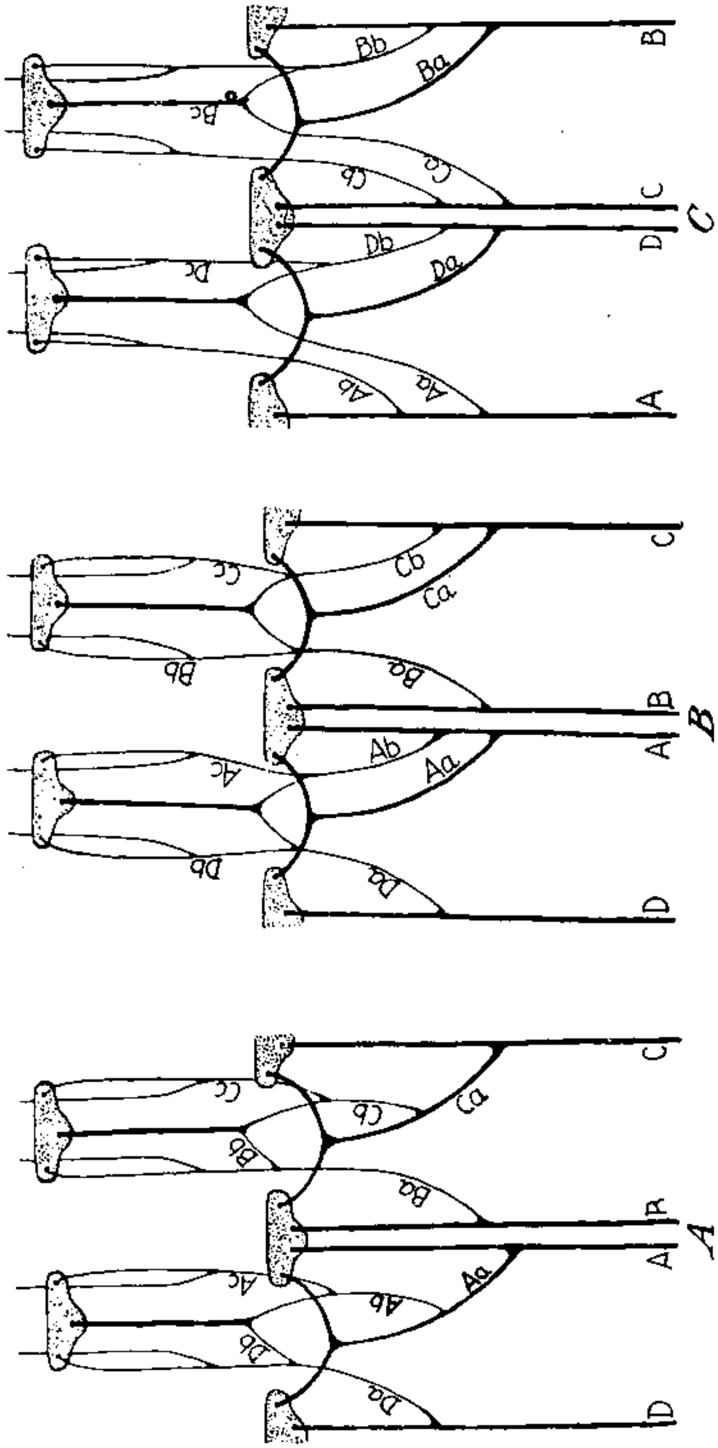
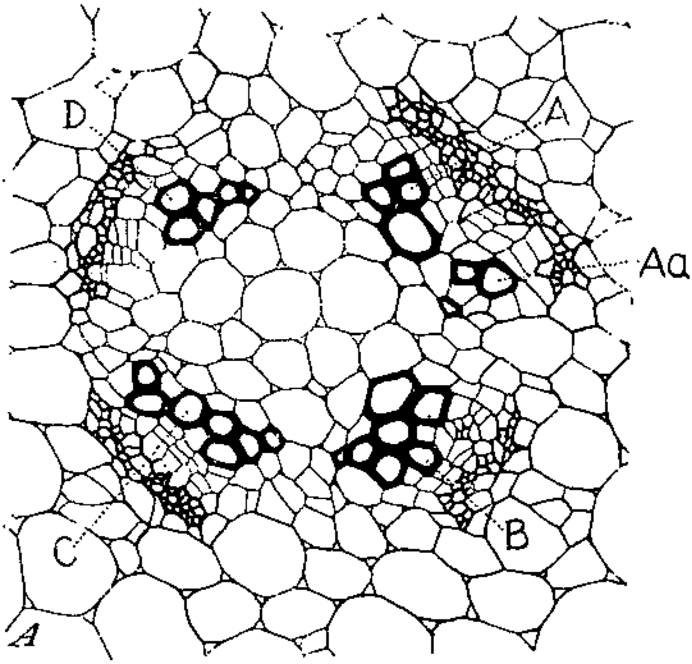


FIGURE 10.—Diagrams showing origin and course of leaf traces in hypocotyl and epicotyl: A, Pattern I; B, pattern II; C, pattern III.



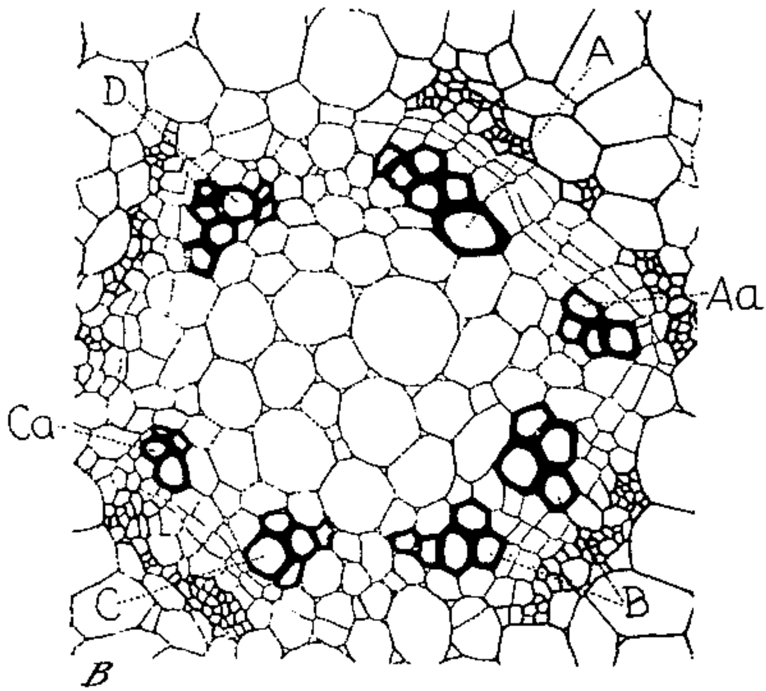


FIGURE 11.—*A*, Cross section through stele of lower hypocotyl showing the widening of bundle A and the splitting off of Aa (see fig. 10, *A*, pattern I). *B*, Cross section near upper hypocotyl showing the splitting off of additional bundles. × 400.

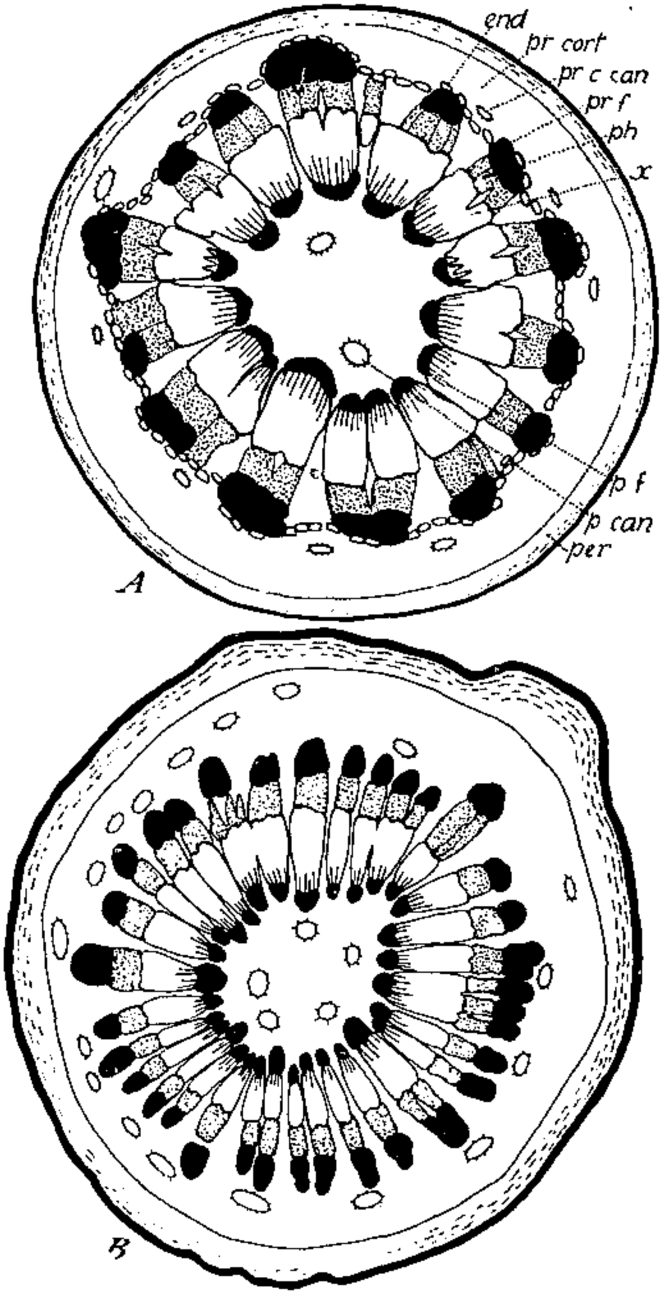


FIGURE 12.—*A*, Diagrammatic drawing of cross section from base of 1-year-old shoot of field plant poor in rubber. × 60. *end*, Endodermis; *pr cort*, primary cortex; *pr c can*, primary cortical canal; *pr f*, pericyclic fibers; *ph*, phloem; *x*, xylem; *p f*, pith fibers; *p can*, pith canal; *per*, periderm. *B*, Comparative section from rapidly growing plant rich in rubber. × 60.

canals in various stages of development belonging to the median and lateral traces of the first two foliage leaves. The mode of origin of these traces is shown in figures 10 and 11 and plate 4. Some of the traces are already split off in the hypocotyl, simultaneous with or immediately following the differentiation of the lateral cotyledonary supply.

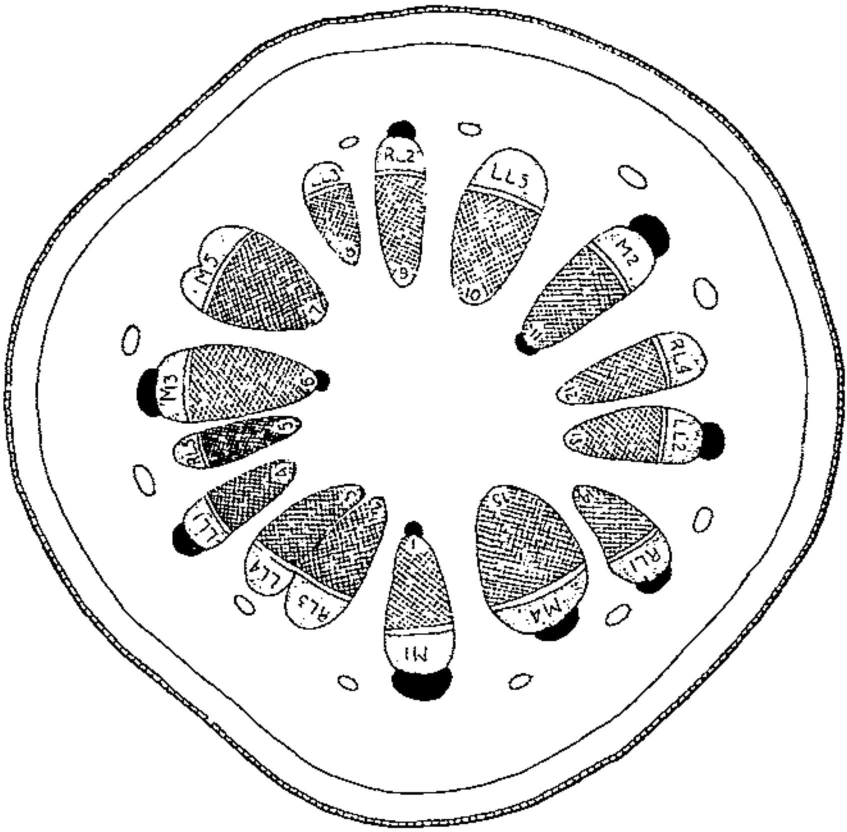
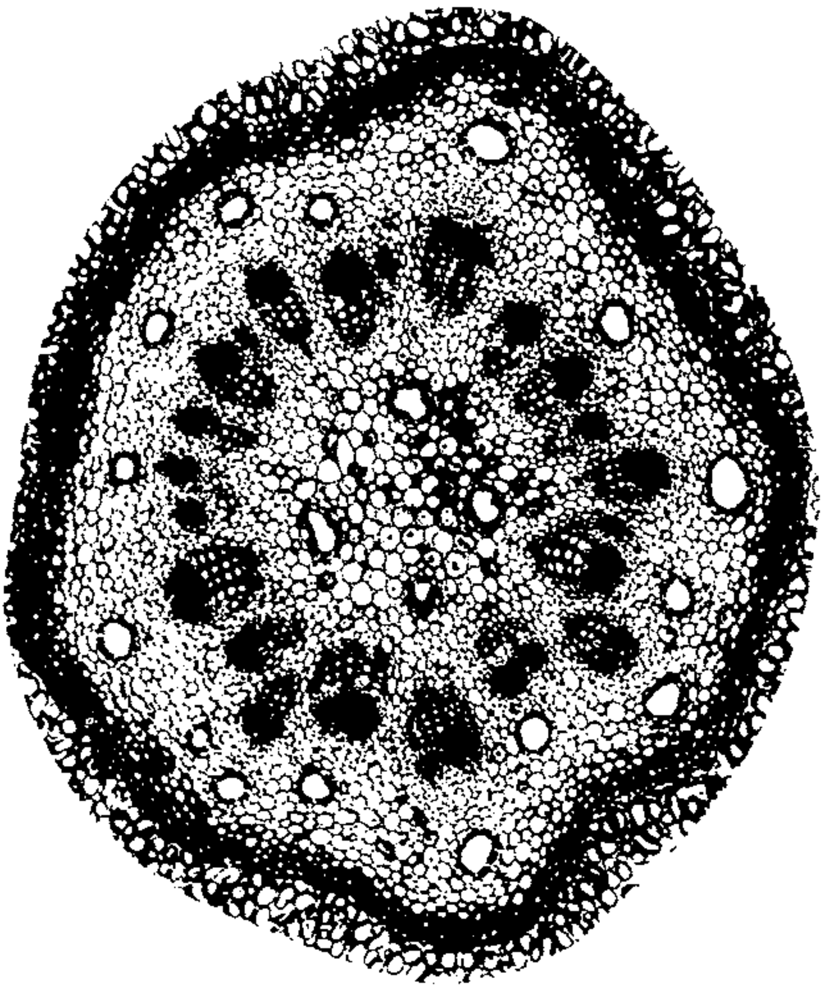


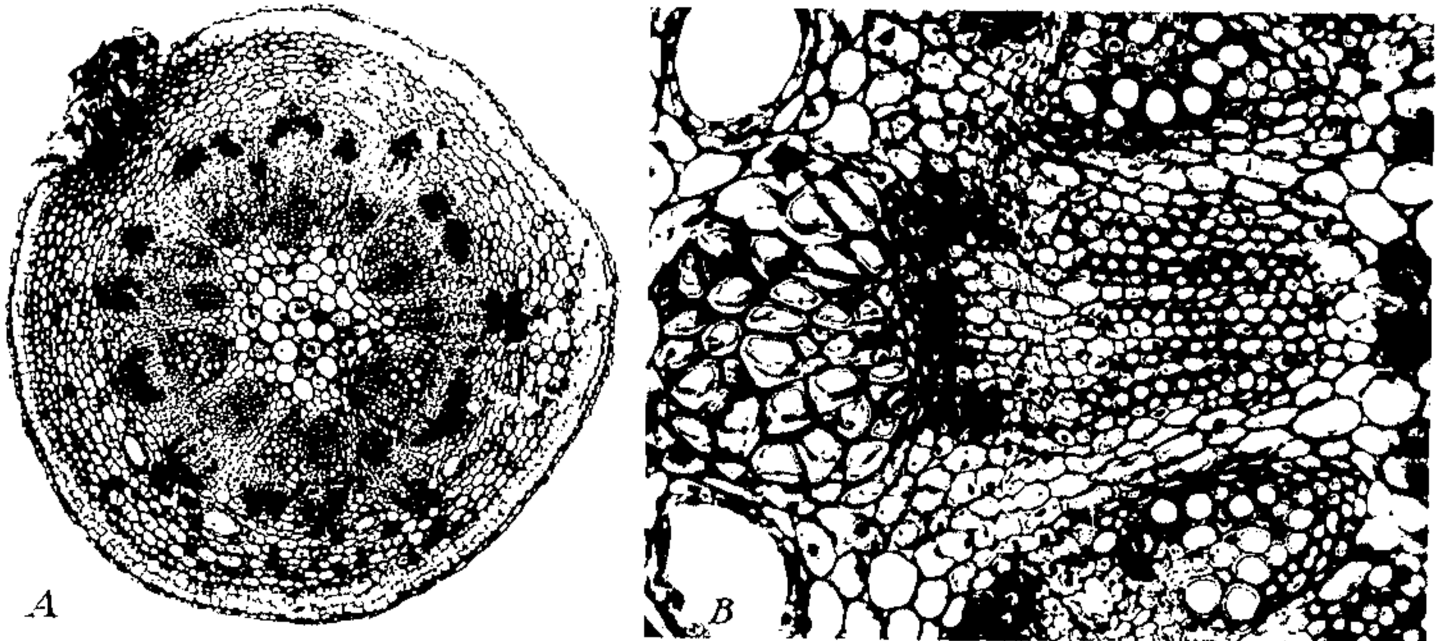
FIGURE 13.—Diagrammatic drawing from base of fifth internode of seedling showing relative position of leaf traces, resin canals, pericyclic and pith fibers: *M1*, median trace of oldest leaf; *LL1*, left lateral trace of oldest leaf; *RL1*, right lateral trace of oldest leaf, etc. The inner numbers, 1 to 15, are consecutive bundle numbers marked down for convenience and without morphological significance. Note that not all 15 bundles run separately throughout their entire course.

DEFINITE STEM

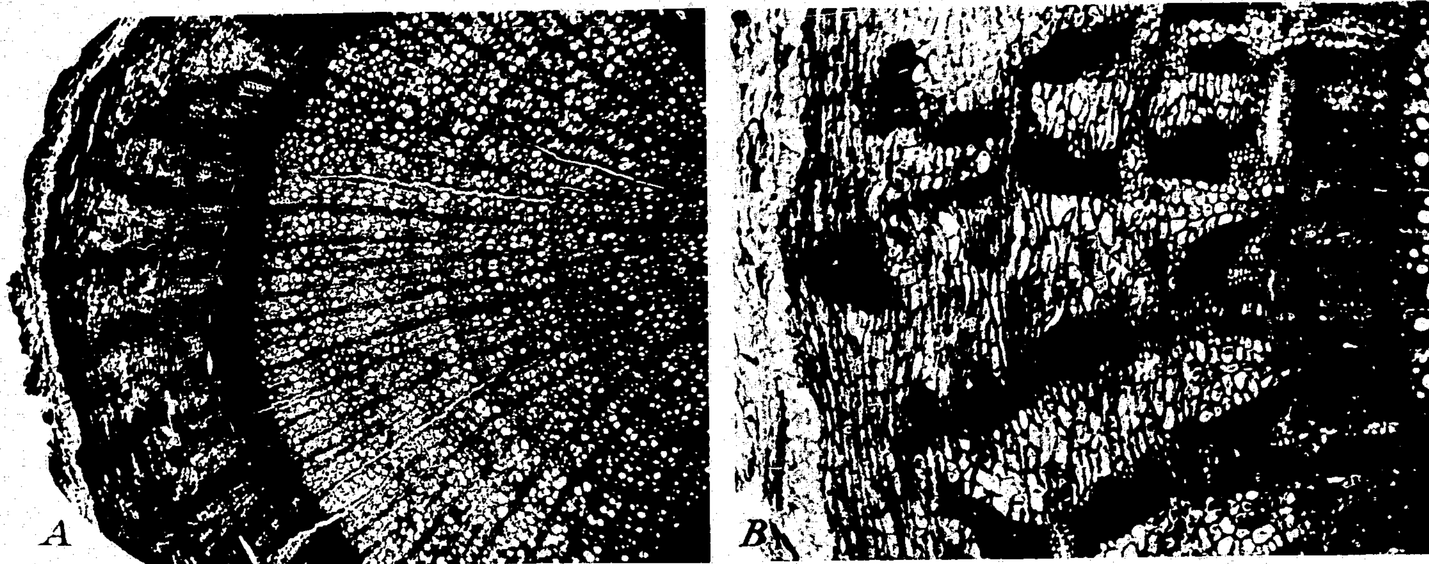
The stem tip of a seedling examined toward the end of the vegetative season differs from the epicotyl in having resin canals in the pith (pl. 6) and fibrous caps around the protoxylem in the region of the perimedullary zone. The number of bundles also is larger and the peripheral rows of cortical cells are distinctly collenchymatous. There is no definite endodermis, but the starch sheath shows up prominently



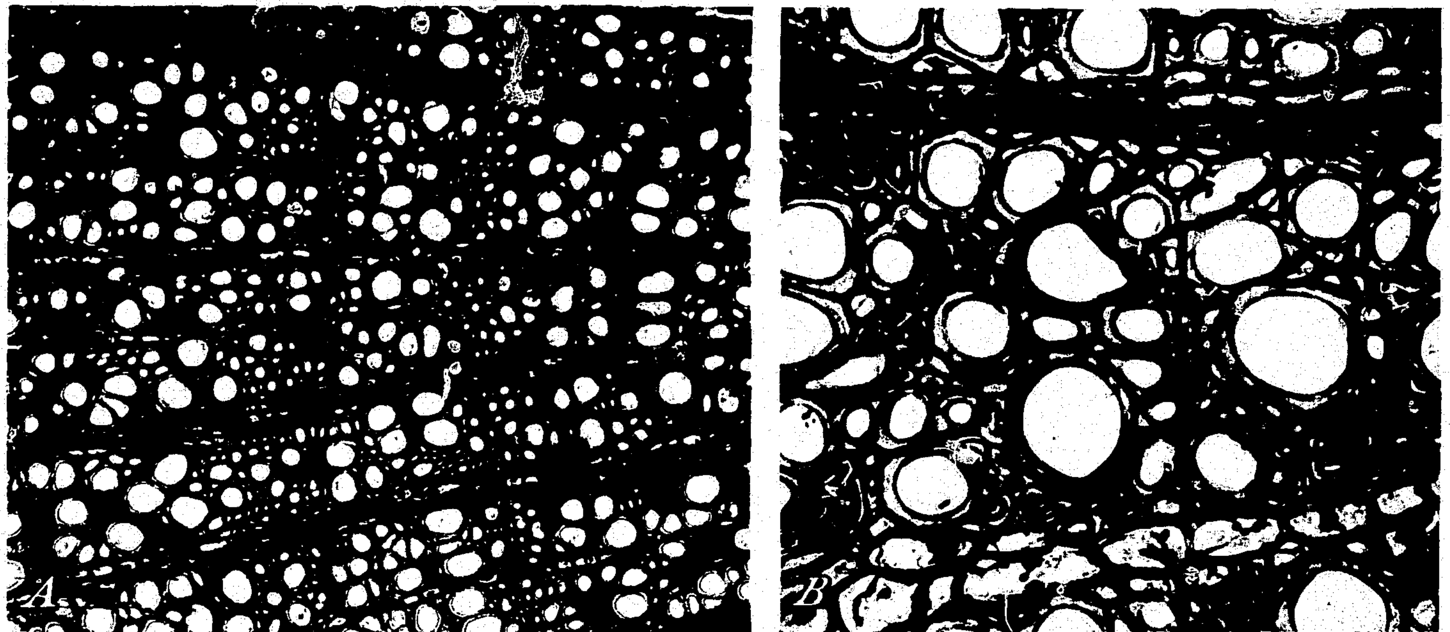
Cross section through apical region of true stem. There are 15 primary cortical canals and 4 pith canals. The outer cortex is collenchymatous, and the epidermis is densely clothed with hairs. × 50.



A, Cross section through the base of the fifth internode of young seedling. (Compare with fig. 11.) Note the development of periderm in the hypodermis. × 144. *B*, Enlarged view of one of the older leaf traces. Note that the xylem of the leaf trace is composed of small elements compared with the large elements in the adjacent younger bundles. × 250.



A, Partial cross section of old stem of field plant. Note massive periderm, broad cortex, and annual ring structure in xylem. Vascular rays are very narrow but flare out funnellike in cortex. × 25. *B*, Enlarged view of cortex. All old phloem has become sclerenchymatous. The resin canals are greatly compressed tangentially. The vascular ray cells of the old phloem are also stretched tangentially after radial divisions had ceased. × 72.



A, Cross section through xylem of old stem of field-grown plant. Vascular rays are uniformly narrow; xylem in general is indistinctly diffuse porous. × 100. *B*, Enlarged view of xylem showing shape of vessels and libriform fibers. × 420.

when fresh stem sections are stained with iodine (fig. 12, *A*). The epidermis is densely pubescent. Periderm development may set in at different levels, often the fifth internode. Its origin is hypodermal (pl. 7, *A*). There are present 11 resin canals flanking the older bundles (fig. 13), but medullary or pith canals are wanting as yet; they are absent from shoots of less than 10 internodes, a fact already mentioned by Lloyd (4). When they are present (pl. 6) their number varies between 2 and 6, with 5 as the most common number. This is in agreement with the type of phyllotaxis that shows a prevalent divergence of 2/5.

The course and derivation of the leaf traces is not at all uniform. The median trace of a given leaf may be a fusion bundle, as in the epicotyl, or a branch of a larger bundle running independently for as many as four internodes.

A cross section through the fifth internode of a shoot shows the relative position of the median and lateral traces of the first five leaves (fig. 13). Fifteen bundles are present. Eight of these, representing the median and lateral traces of the older leaves, have caps of primary pericyclic fibers above the phloem and three have, in addition, perimedullary caps (bundles 1, 6, 11 in fig. 13). To be sure, not all the 15 bundles shown in figure 13 run separately and independently throughout their entire course. Some anastomose and fuse, and others split to form the traces of later departing leaves. Of interest is the structure of the xylem of the older leaf traces. In these the xylem is composed altogether of small spiral elements contrasted with the large xylem cells in the adjacent younger bundles (pl. 7, *B*).

ANATOMY OF MATURE STEM

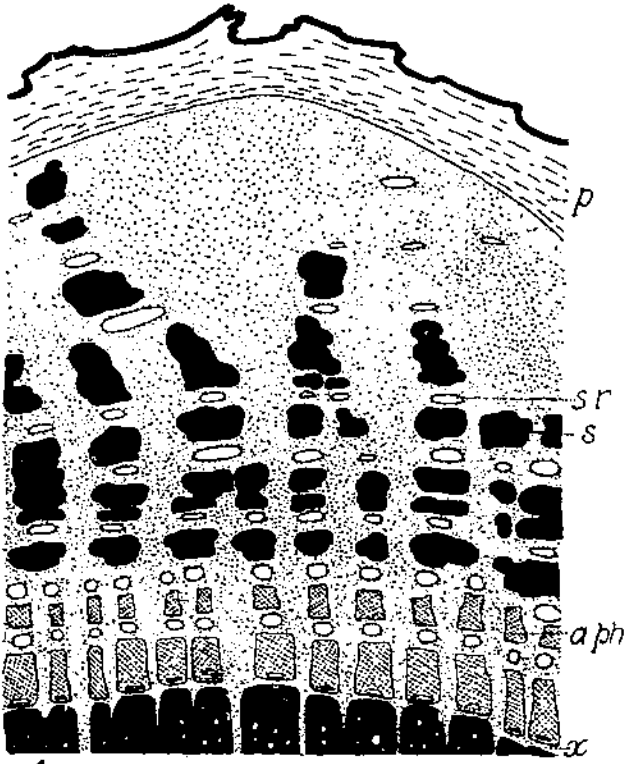
General Structure

A cross section of a stem of harvest size (pl. 8, *A*) shows a dense woody core and a broad cortex limited externally by an irregular massive periderm.

The wood is made up of a series of concentric or excentric rings, each of which represents, in normally developed plants, the annual increment of wood. Stems frequently show a banded appearance in cross section. The bands follow the general contour of the annual rings, but they are not identical with them. In general, the annual rings are poorly defined and very narrow. Frequently they vary in width in different parts of the circumference of the stem, at a given level. Also, in response to abnormal distribution of rainfall, additional annual rings may be formed. This makes the practical value of rings as indicators of age of plants very uncertain.

The pith is very small and, although it enlarges considerably in older plants, it is usually less than 0.4 mm. in diameter. In old stems the pith may become in part sclerotic.

The cortex comprises all tissues outside the cambium. It consists principally of secondary phloem, both functional and old, together with vestigese of the primary cortex. Under low magnification it ap-



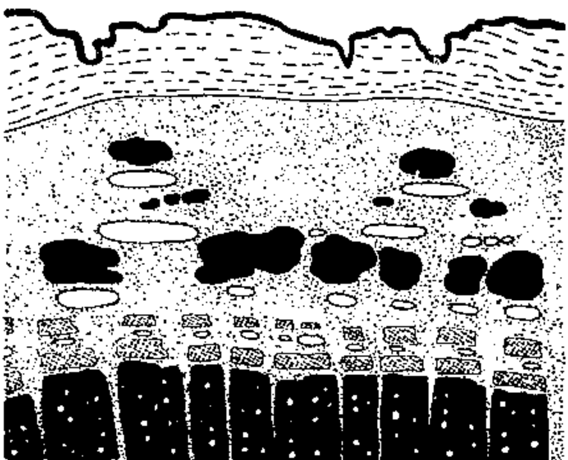
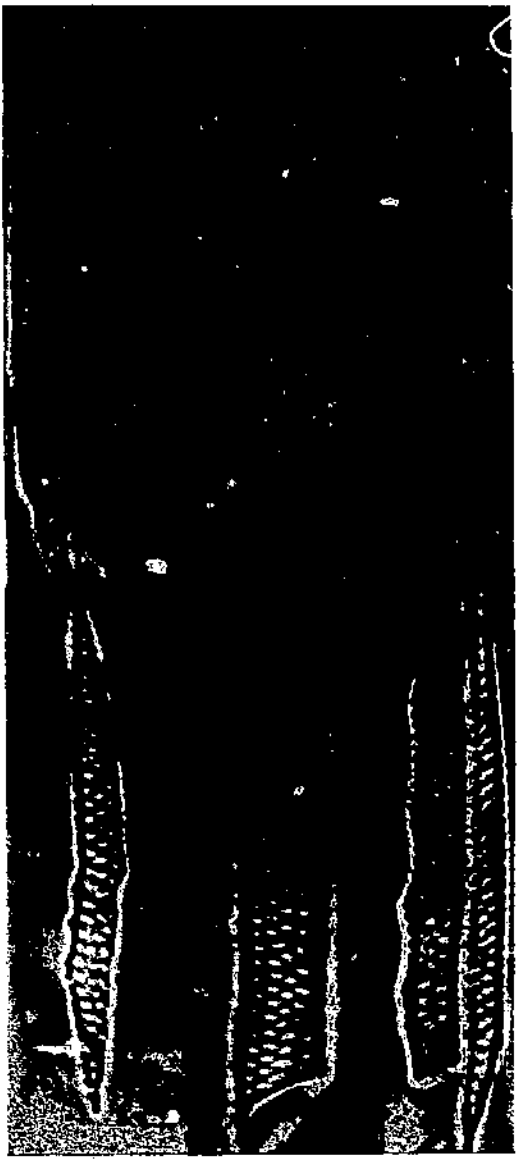


FIGURE 14.—A, Diagrammatic drawing through secondary cortex of large stem. × 40. *p*, Periderm; *sr*, secondary resin canal; *s*, group of sclerenchyma; *a ph*, active phloem; *x*, xylem. *B*, Drawing of secondary cortex of large secondary root. × 40. Note that the cortex is not nearly as wide as in the stem, that the groups of sclerenchyma are fewer, and the phloem groups are stretched tangentially rather than radially.



Various types of vessels obtained by maceration of wood with nitric and chromic acid (10 percent). × 500.

A, Tangential section through cambium and young phloem. × 110. Note tiered arrangement of cambium cells and beading of radial walls. *B*, Radial section of cambium, resin canals, and phloem. × 110.

pears to be made up of irregular concentric layers of fibers and resin canals alternating with one another and embedded in parenchymatous ray tissue (pl. 8, *B*, and fig. 14, *A*). In the region of the cambium the phloem consists of thin-walled tissue containing usually one ring of resin canals.

The protective corky layer or periderm is massive and irregular, often showing deep notches in transverse stem sections and irregular fissures in surface view. In varieties high in rubber the periderm is usually thin. Lenticels are fairly abundant. Deep cracks and places of injury are often marked by escaping resin that collects in drops on the wound.

Xylem

The xylem is indistinctly diffuse porous with the pores often grouped in a manner to simulate a ring porous condition (pl. 9, *A*). The pores are barely visible to the naked eye, and the vascular rays are invisible on both cross and longitudinal sections.

The pores or vessels are fairly numerous, round, elliptical or somewhat angular, solitary or in multiples of two or more (pl. 9, *B*), varying in size from 11μ to 54μ. Vessel members are cylindrical or fusiform to irregular in shape (pl. 10), with or without ligular projections beyond the perforation plates, from very short (75μ) to medium long (185μ). Perforation plates are horizontal or oblique, the perforation simple. Lateral walls have numerous slightly alternately arranged pits, borders broadly elliptical, horizontal, or slightly oblique. The lateral walls in all vessels have tertiary thickening. Older vessels sometimes develop tyloses, and the lumen of others may contain "gum plugs."

Wood parenchyma is sparse, indistinctly terminal and paratracheal but never forming complete sheath around vessels; cells are elongated and usually pointed. Pits small, simple, numerous on vertical walls in contact with vessels but wanting on wall bordering fibers.

Fibers are of libriform type forming ground mass of wood, fairly uniform in transverse section, tapering gradually with smooth, toothed or forked ends. They are relatively short (less than 250μ), walls very thick, lumina round, deltoid, elliptical or slitlike in transverse section. Pits not numerous, bordered with oblique, slitlike apertures.

Vascular rays are closely set and numerous, usually very tall, slightly heterogeneous. In transverse section the ray cells are radially elongate but variable, in tangential section two to four cells wide at middle; marginal cells as well as body cells angular elliptical; all cells medium thick, pits simple and very numerous. In very old stems the most centrad part of the rays may be lignified wholly or in part.

Phloem

Active Phloem

The functional secondary phloem of guayule, like that of many other woody plants, is a complex tissue made up of a number of cell types all of which have a common origin in the cambium. The cells of the latter are brick-shaped in transverse section and fusiform in tangential section (pl. 11, *A*); they are arranged in definite horizontal rows. In radial section (pl. 11, *B*) the cells are very narrow, and the end walls are square. The radial walls are much thicker than the tangential walls and appear prominently beaded (pl. 11, *A*), that is, showing abundant pitlike thin spots.

The elements that comprise the secondary phloem are sieve tubes, companion cells, and phloem parenchyma. They form more or less uniform radial sectors (pl. 12), radiating centrifugally from the cambium and separated from one another by rays that are continuous with the vascular rays of the xylem. The tiered arrangement of the cambium cells noted above is maintained to a certain extent by the sieve tubes and phloem parenchyma cells (pl. 11, *B*).

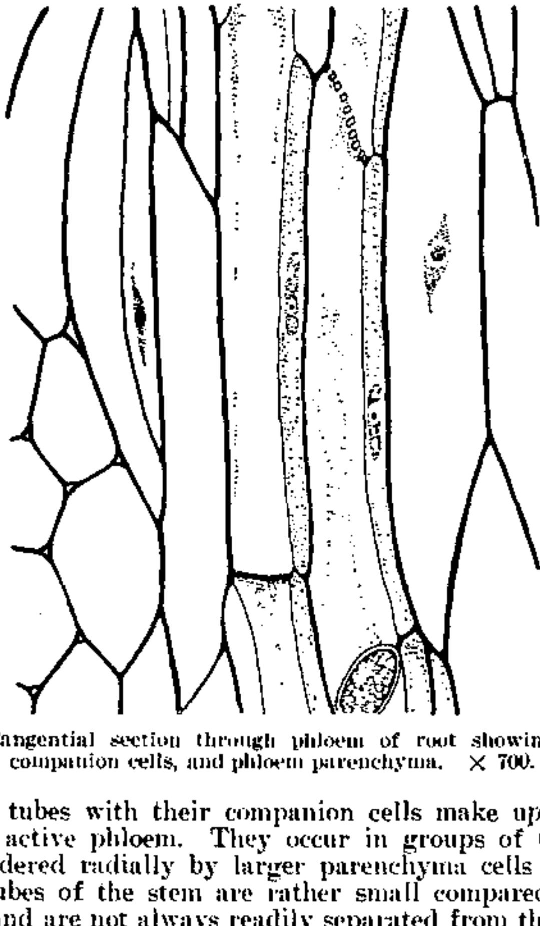
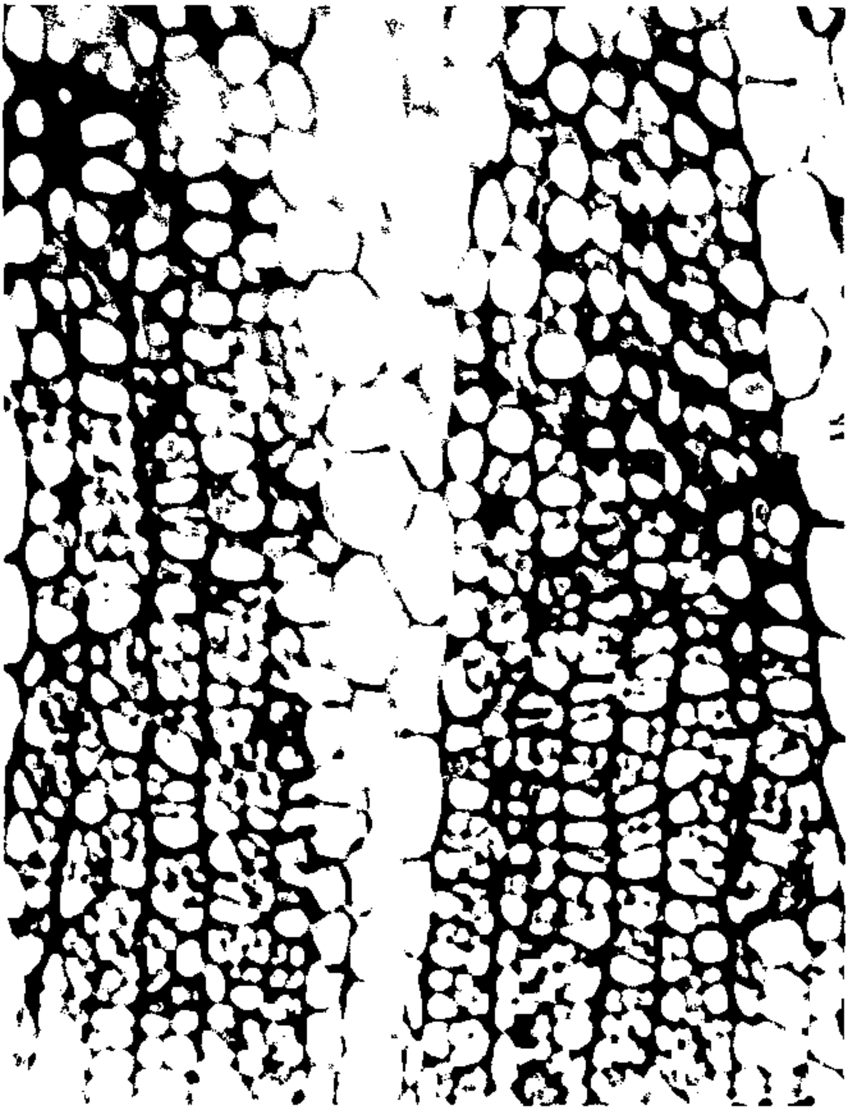


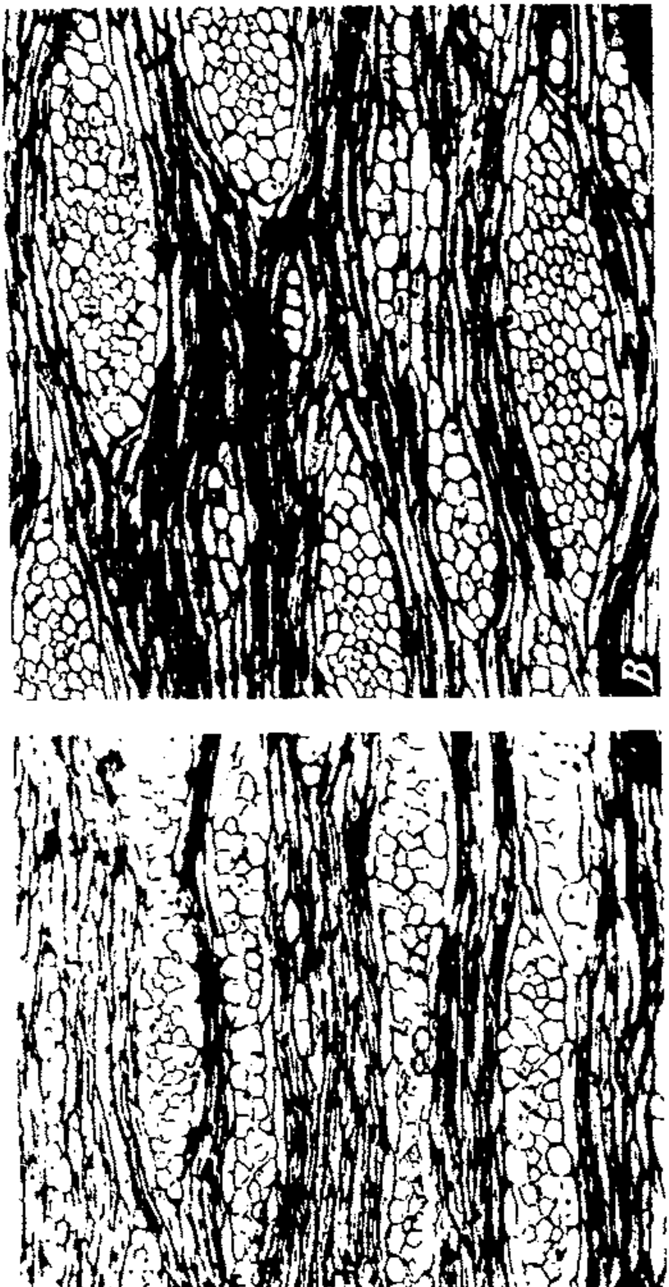
FIGURE 15.—Tangential section through phloem of root showing sieve tubes, companion cells, and phloem parenchyma. × 700.

The sieve tubes with their companion cells make up the greater part of the active phloem. They occur in groups of two or more and are bordered radially by larger parenchyma cells (pl. 13, *A*). The sieve tubes of the stem are rather small compared with those of the root and are not always readily separated from the companion cells in transverse section. The end walls of the sieve tubes are somewhat oblique, or the sieve plates are strictly transverse (fig. 15). There is commonly one sieve field with numerous small pores but occasionally two sieve fields are observed, and in such case the end wall is steeply sloping. The lateral walls of the sieve tubes are without lattices.

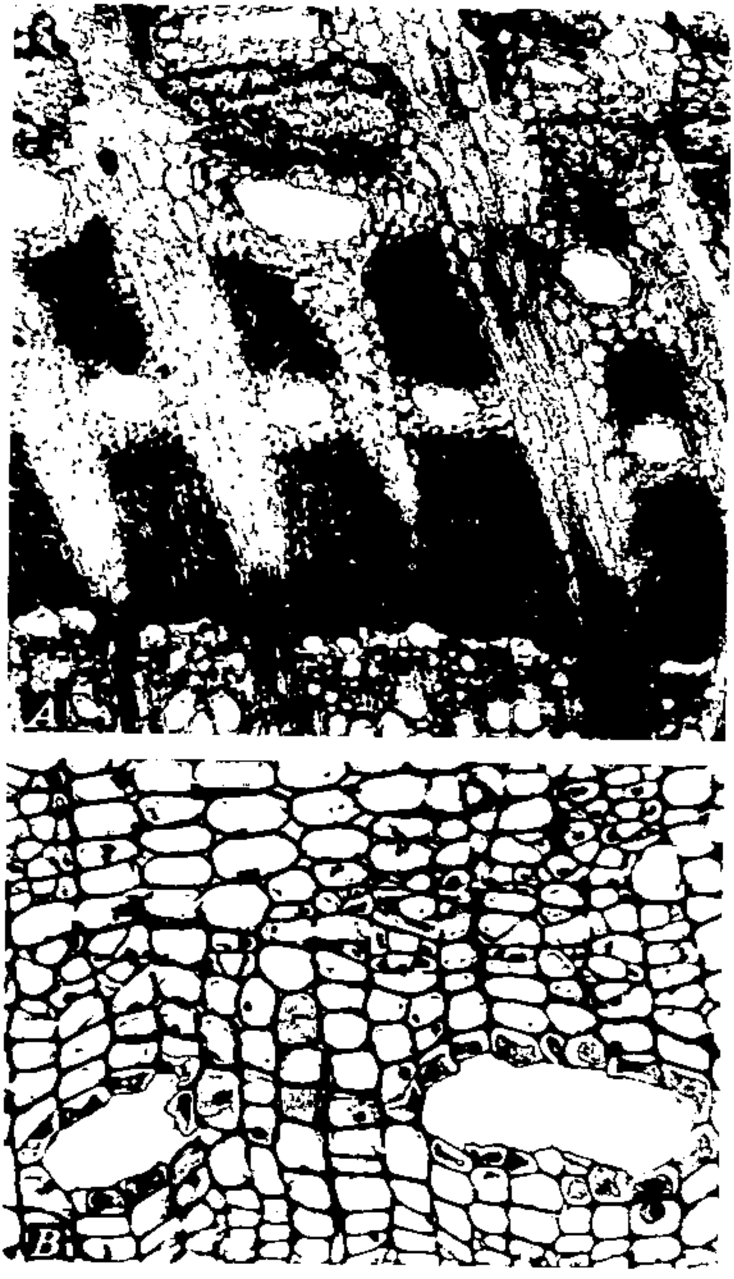


Cross section through two groups of active phloem separated by a vascular ray. The phloem parenchyma cells are recognizable by their lack of content and large size. The size increases toward the top of the illustration, and some of the parenchyma cells of the bundle on the left side already have matured into fibers. × 225.

A, Enlarged partial view of plate 12 showing in greater detail the sieve tubes with their companion cells and phloem parenchyma. × 950. *B*, Radial section of young but already inactive phloem of root. Note the prominent latticelike pitting of the radial walls. Sieve tubes and companion cells already are crushed. × 700.



A, Tangential section of active phloem of stem. Note height and width of vascular rays; also structure of ray cells. × 110. B, Tangential section of active phloem of root. Note that the vascular rays are less high and broader. × 110.



A, Hand section through active phloem of old stem. Note that the active phloem represents two growth increments. × 70. B, Cross section through cambium and outer phloem region of root to show relation of resin canals to cambium. Epithelial cells of canal abut directly on cambium. × 370.

Although several sieve tubes may abut on each other there is normally one companion cell to a sieve tube, extending the entire length of the sieve tube element to which it is adjacent (fig. 15). According to Vuillemin (*7*) the sieve tubes of the Compositae are of a much larger transverse diameter than the companion cells, but Lloyd (*4*) holds that this is not true of *Parthenium*. According to Lloyd "there is but little difference in transverse diameter of these, the companion cell being narrowly fusiform and therefore thickest at the middle, while the reverse, of course, is true of the sieve elements." However, in the investigations reported in this bulletin, there is a difference in size between these two elements and, although this difference is not very pronounced in the phloem of the stem, it is conspicuous in the phloem of the root, as will be shown later.

The phloem parenchyma cells are of the cambiform type and in tangential section look very much like the cambium cells from which they are derived. They are profusely pitted radially, with the pits arranged in sievelike groups. The cells enlarge as they grow older, but the walls do not thicken until toward the end of the season. There is no difference between the phloem parenchyma cells and the sclerenchyma initials, since most of the cells are pointed and eventually thicken and lignify. The parenchyma cells surrounding the epithelial layer of the resin canals contain large starch grains, like the endodermis. Occasionally starch is found in the parenchyma cells inside the endodermis, sometimes forming single radial rows along the flanges of the outermost group of fibers connecting the endodermis with the jacket cells of the first secondary resin canals.

The ray tissue of the phloem is continuous with the vascular rays of the xylem (pl. 8, *A*). The rays are in the beginning as wide as the xylem rays, but they sharply increase in width outwardly (pl. 12). This widening of the ray is the result of increase in cell size toward the outer end of the ray as well as some increase in the number of cells. In a cross section of a stem the ray cells appear elongated radially, but distally there is much tangential stretching to compensate for the increase in circumference caused by the enlarged diameter of the axis. In tangential section the ray cells appear round or angular (pl. 14, *A*), with the marginal cells usually larger and more elongated. The tangential walls are heavily pitted, the pits arranged in sievelike groups.

SECONDARY RESIN CANALS

The ontogeny of the secondary resin canals has been given in detail by Ross (*5*) and Lloyd (*4*). The canals are schizogenous in origin, and in that respect resemble the primary cortical and pith canals. They are derived directly from the cambium (pl. 15, *B*). The two cell layers split away, and the tangentially flattened space gradually becomes spherical. The cells bordering the canal form the epithelium or secretory layer; they are brick-shaped in cross section and elongated rectangular longitudinally and are easily recognized by their dense protoplasmic content and large nuclei. Occasionally, prior to the formation of the canal, the epithelial initials divide periclinally, producing an additional layer of cells. This layer lacks the protoplasmic content of the secretory layer but differs from the adjacent phloem parenchyma cells. The fully developed resin canal is usually spherical; it may retain this shape or become compressed tangentially as the phloem becomes inactive and sclerenchyma develops. According to Lloyd (*4*), the canals become frequently closed by an ingrowth of tissue that resembles a bunch of grapes. Such extensive "pseudotyloses" development has not been observed in the material available for study, but trichomelike structures proliferating from the cells of the secretory layer have frequently been noticed (pl. 11, *B*). The jacket of parenchyma cells surrounding the secretory layer of the canal is from one to several cells wide. These cells are filled with starch but contain little rubber, as will be shown later.

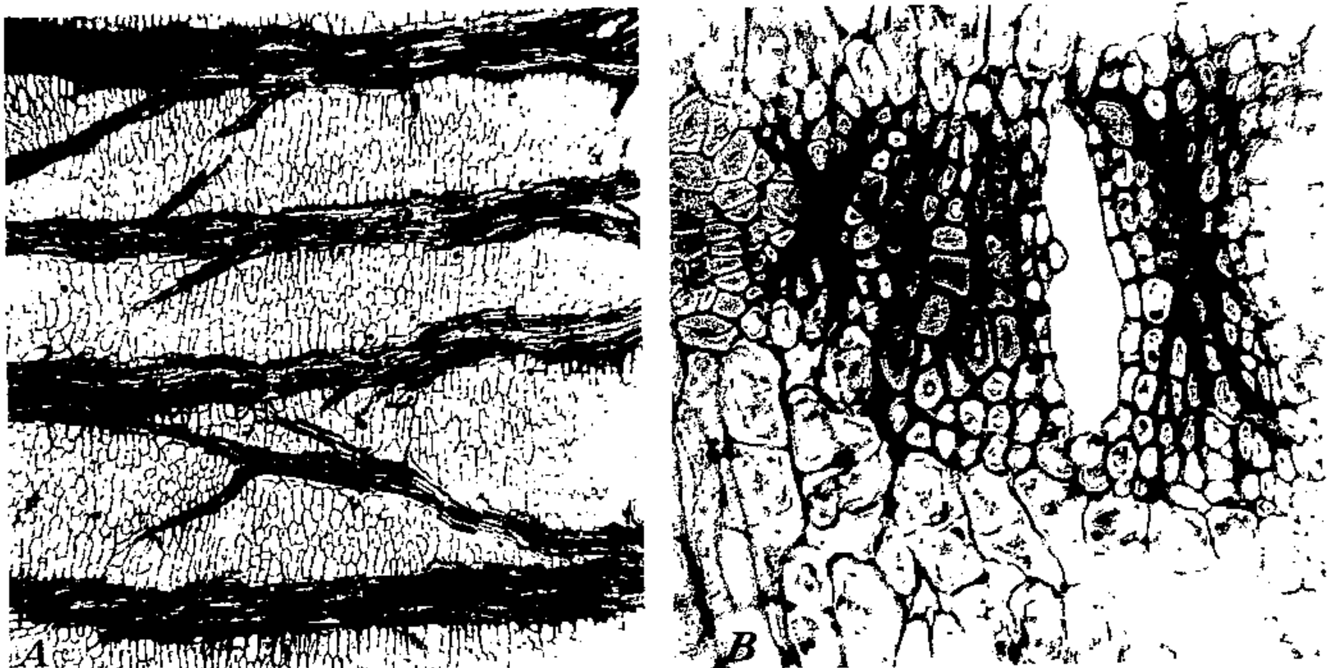
INACTIVE PHLOEM

Cessation of activity in the secondary phloem is gradual. In the young stems the sieve tubes may function for a single season only, but the phloem of the large branches may retain a normal structure for two complete seasons (pl. 15, *A*), except for the formation of callus deposits over the sieve plates. Sometimes toward the end of the growing season some of the phloem parenchyma cells or sclerenchyma initials become thick-walled and lignify (pl. 12). Lignification of the phloem parenchyma is usually centrad from the outer margin of the season's growth, but, in material where the phloem remains structurally unchanged for two seasons, solitary lignified cells or small islands of thick-walled fibers may occur sporadically in the midst of otherwise normal-appearing phloem. The phloem fibers vary greatly in size and shape; some are typical pointed fibers, others are broad, spindle-shaped, and some have more or less square end walls. The phloem fibers vary in thickness between 15μ and 70μ, and in length between 160μ and 640μ. The peripheral cells of the first ring of fibers are usually very large and more like stone cells in character, having been derived from cells of the ray tissue.

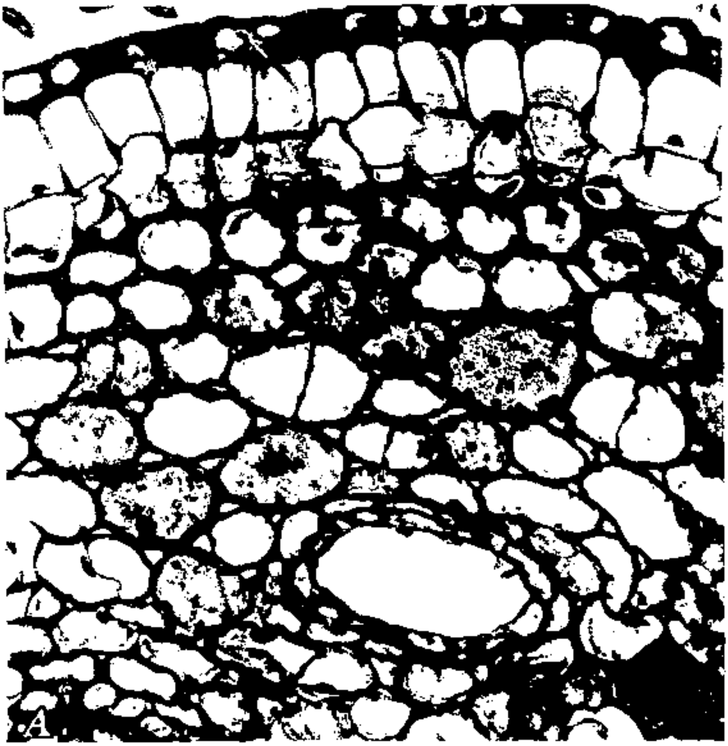
With the progressive enlargement and lignification of the fibrous elements, the sieve tubes and companion cells are crushed. The collapse of these elements is usually so complete that the crushed cells are represented only by an irregular band of wall substance (pl. 16, *B*), but the fibers come to occupy the entire area of formerly active phloem recognizable in tangential section by deeply staining anastomosing bands against a background of small-celled vascular ray tissue (pl. 16, *A*).

PERIDERM

The periderm or cork consists of two layers of tissue, phellogen and cork. No phelloderm is formed toward the inside. The phellogen or cork cambium arises in the hypodermis (pl. 7, *A*, and pl. 17, *A*). Sometimes this layer divides only once, forming a superficial periderm, while a subhypodermal layer takes over the function of the phellogen. The cork cells are of the common type, made up of three layers, but the walls remain quite thin. Since cork tissue is relatively inelastic, the periderm develops shallow or deep cracks as the stem increases in diameter (pl. 17, *B*). These fissures in the cork may extend as deep as the peripheral resin canals, causing the resin to ooze out and collect in small droplets on the outer surface.



A, Tangential section through inactive phloem. The sieve tubes and companion cells have been crushed and all parenchyma has become sclerotic. The tissue back of the strands of fibers is vascular ray tissue. × 45. *B*, Cross section through inactive secondary phloem. The blackened areas between the fibers represent the crushed sieve tubes and companion cells. The resin canals are compressed tangentially, but the epithelial cells and the one-celled parenchymatous jacket are unaffected.



A, Cross section through young stem showing hypodermal origin of periderm. × 400. *B*, Cross section through old periderm of root. Note the deep cracks in the cork. × 100.

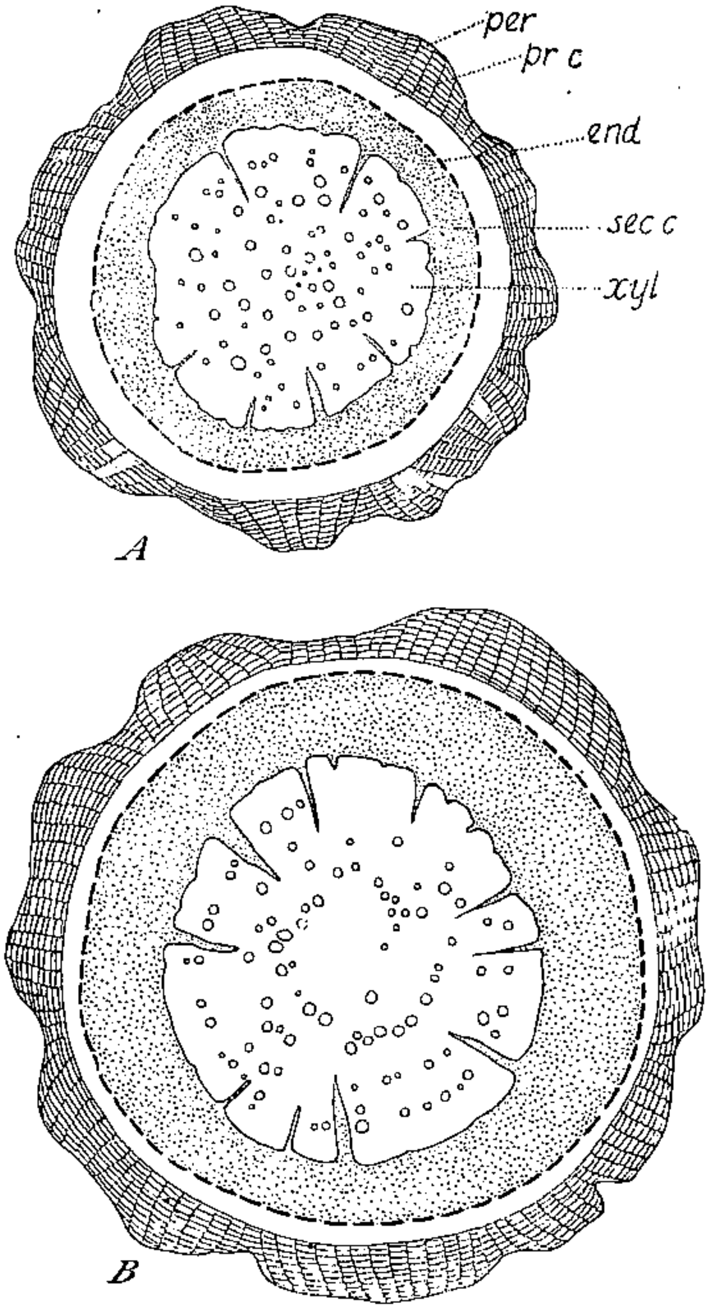


FIGURE 16.—*A*, Diagrammatic drawing of cross section of lateral root 2.7 mm. in diameter; *per*, periderm; *pr c*, primary cortex; *end*, endodermis; *sec c*, secondary cortex; *xyl*, xylem. *B*, Drawing of larger root 3.8 mm. in diameter.

The original superficial periderm may persist for the life of the plant when grown in a commercial plantation. In its natural habitat, where plants commonly become older, cork cambiums may be formed progressively inward, gradually cutting off all vestiges of primary cortex. Quite often new phellogen layers develop internally in localized regions, cutting out shell-shaped layers of primary and peripheral secondary cortex. Such regional deep-seated cork development is quite commonly the result of wounding, and is, therefore, met with even in young stems.

ANATOMY OF ROOT

The root system consists chiefly of long, medium thick, and thin laterals diverging at right angles from the taproot (fig. 2). The roots are yellow in color, and the surface is mottled or roughened by shallow longitudinal fissures.

Cross sections through such roots exhibit a hard, pithless, woody core and a broad cortex protected by a massive periderm that is radially segmented by deep cracks (fig. 16, *A*, *B*). The relative thickness of this cork layer is not correlated with the diameter of the root, being prominent in thick laterals as well as thin tertiaries. Only fibrous roots less than 1.5 mm. in diameter lack a periderm but possess a dense covering of root hairs, turgid and functional up to the insertion point of the rootlet on a larger lateral or even the main root. These apparently long-persisting root hairs should facilitate the rapid absorption of water, even from superficially wetted soils.

The wood is very hard; the central core, corresponding in size to the pith of the stem, is especially dense (pl. 18, *A*), and from its periphery the vascular rays are seen radiating toward the cortex.

The cortex is massive but not nearly so broad as in the stem (fig. 14, *B*). It is made up of concentric layers of resin canals and fibers embedded in parenchymatous ray tissue.

XYLEM

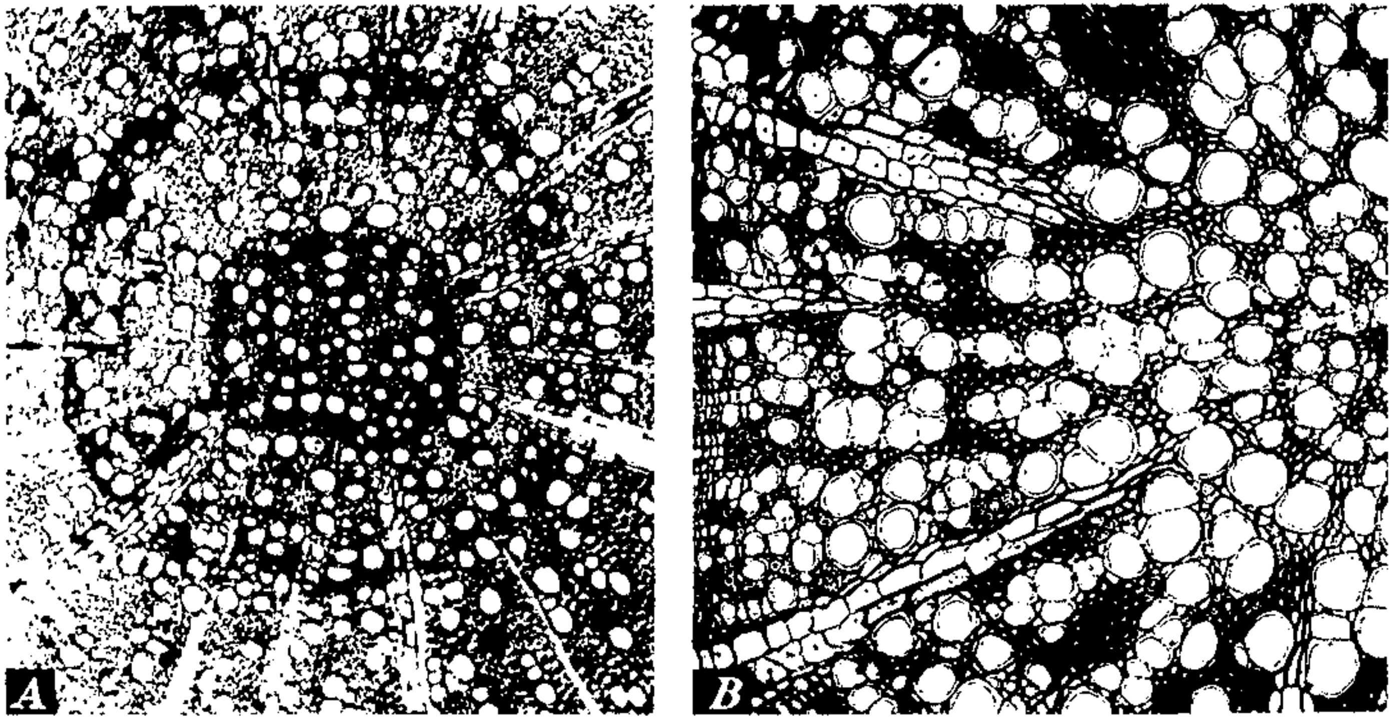
Since the elements making up this tissue are quite similar to those of the stem, a detailed description will not be given.

The xylem is indistinctly diffuse-porous, with the pores less numerous than in the stem except in the region of the central core (pl. 18, *B*). The vessels are frequently arranged in short radial rows that often border on the vascular rays (pl. 19, *A*), enclosing bands of fibers. The latter form the ground mass of the wood even more so than in the stem. The cells are always thick-walled and sparsely pitted. Wood parenchyma is paratracheal and sparse.

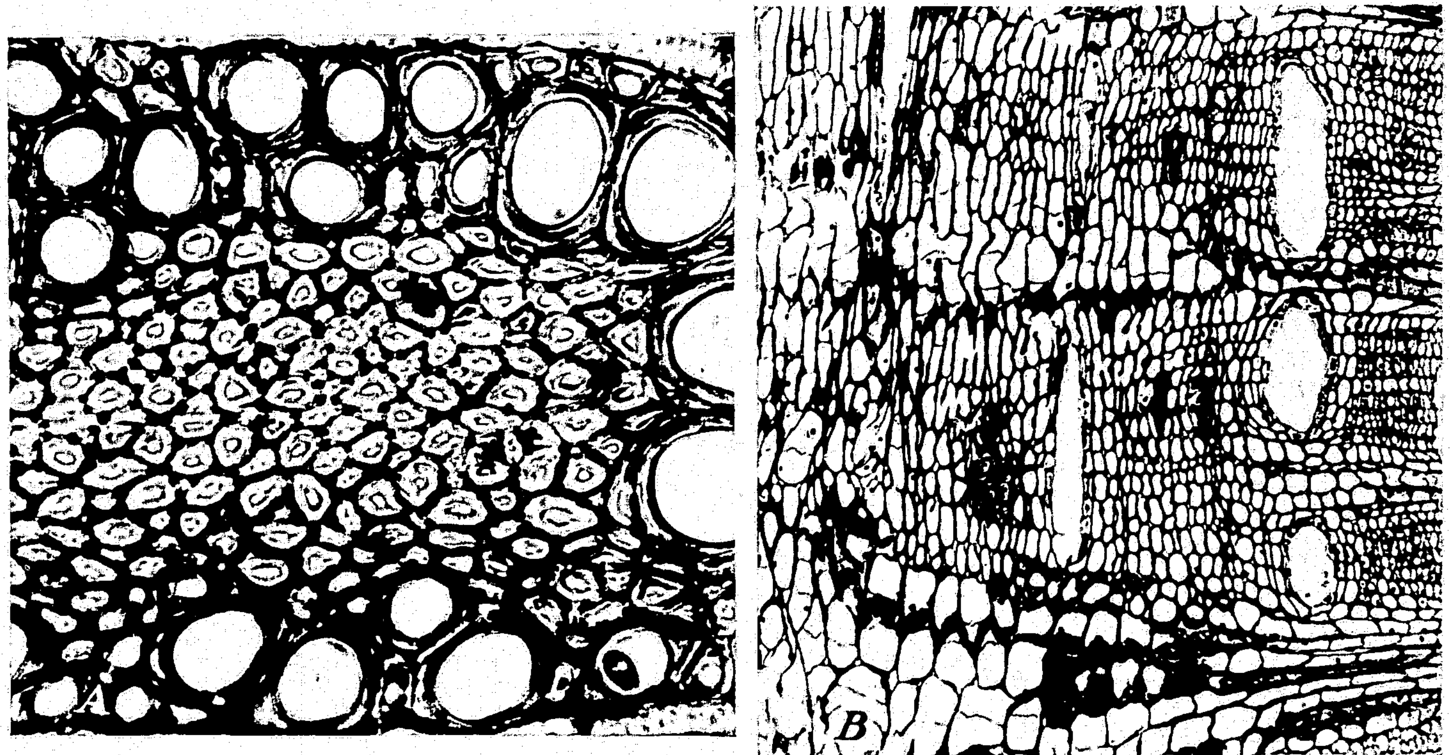
The vascular rays are farther apart and broader than the rays in the stem. Most of them are very tall, so that many of the primary rays form uninterrupted radii from the central core to the cambium.

PHLOEM

As in the stem, the cortex comprises the band of tissue between cambium and cork. It consists of a narrow ring of primary cortex and a broad zone of secondary phloem with vestiges of primary



A, Cross section through central part of large root. Note the dense central core and dark staining of first annual ring. × 75. B, Cross section through central part of younger root. The vessels near the center are large and very numerous. × 200.



A, Enlarged section of xylem of old root. The large vessels are arranged in radial rows on either side of the vascular rays enclosing a large group of dense libriform fibers. × 420. *B*, Cross section through active and old phloem of medium-sized lateral root. The phloem groups delimited by vascular rays are broader than those in the stem phloem (compare pl. 13); the resin canals are also tangentially wider and there is little fiber development. × 110.

phloem occasionally recognizable in younger roots. Since the cambium in the roots of guayule is hypodermal in origin and remains active for a very long time, the primary cortex persists, although in altered form, even in fairly old roots (fig. 16, *B*); its inner contour is easily delimited by following the deeply staining Casparian strips of the endodermis. In young roots, the primary cortex is fairly prominent (fig. 16, *A*), but as the root enlarges and secondary phloem becomes more massive, the cortical cells are stretched tangentially, anticlinal divisions become fewer, and the cell lumen is obliterated, making it increasingly difficult to separate this layer from adjacent tissues.

ACTIVE SECONDARY PHLOEM

The groups of active secondary phloem are not radially elongated as in the stem (fig. 14, *A*), but appear broader tangentially (fig. 14, *B*); also the groups are less distinctly delimited from the vascular rays.

The phloem is made up of sieve tubes, companion cells, and phloem parenchyma. The sieve tubes are larger than those of the phloem in the stem, and there is a conspicuous difference between the size of the sieve tubes and companion cells in cross section (pl. 20, *A* and *B*). Phloem parenchyma cells are elongated rectangular in radial section, and the walls are heavily pitted (pl. 13, *B*).

The vascular rays are continuous with those of the xylem. They are broader than the rays in the stem and become even more conspicuous by spreading out fanlike soon after they enter the phloem (pl. 19, *B*). Some of the smaller secondary rays end blindly, because each newly differentiated ring of resin canals has a larger number of canals than the older ring. In such places two resin canals appear in juxtaposition with a single older one, and the vascular ray between these canals and the phloem groups centrad to them terminates just below the older canal (pl. 19, *B*).

The resin canals in the secondary phloem of the root are rarely spherical but oval, often reduced to mere slits in the older part of the cortex. The canals are commonly surrounded by several rows of parenchyma cells derived from the cambium, though occasionally periclinal divisions in the epithelium may contribute locally to this jacket.

OLD PHLOEM

Cessation of activity in the secondary phloem of the root appears to be more gradual than in the stem, since fiber differentiation, so prominent a feature of the phloem of the stem, is much less pronounced here and in places altogether wanting (fig. 14, *B*).

In the stem, rings of resin canals alternate with bands of fibers, but in the root two rings of resin canals often intervene between rings of fibers, though frequently small groups of sclerenchyma are interpolated locally between rows of resin canals (pl. 19, *B*). Retrogressive changes in the older phloem tissue, whether accompanied by differentiation of sclerenchyma or not, go on as in the stem. Sieve tubes and companion cells collapse, and their former location is indicated only by certain thickened regions in the cell wall (pl. 19, *B*).

Phloem parenchyma cells may enlarge without apparent thickening of their walls, or they become sclerenchymatous wholly or in part. These groups of sclerenchyma or fibers have a greater tangential than radial extent. Sometimes adjacent groups will coalesce, in which case neighboring ray cells also become sclerotic.

Although retrogressive changes in the phloem of the root are not so pronounced as in the stem and are later to appear, the active life of the secondary phloem probably is the same as in the stem. Callus plugs over the sieve plates become evident at the end of the growing season, and, with the advent of new growth, the old sieve tubes become obliterated and collapse while the surrounding parenchyma cells enlarge and often lignify.

STRUCTURE OF THE PEDUNCLE

The peduncle or main shoot of the inflorescence is exceedingly slender and may attain a length of 20 cm. Anatomically it is characterized by an excessive development of mechanical tissue which jackets the rather weakly developed vascular bundles, often completely. In transverse section the peduncle appears fluted, with narrow collenchymatous ridges alternating with broad strips of chlorenchyma. The epidermis covering the collenchyma ridges is composed of elongated pointed cells, but the epidermal cells in the depression between the ridges are short, irregular, and contain stomates. T-shaped hairs, typical of the pubescence of leaf and stem, clothe the entire outer surface.

Cortex and pith are similar in structure to those of young stems except that in mature peduncles solitary cortical cells may become thick-walled and lignify while the pith may become lignified in part. A periderm as reported by Lloyd (*4*) has not been observed.

The peduncle lacks resin canals in the pith but has a regular complement of these in the cortex.

STRUCTURE OF THE LEAF

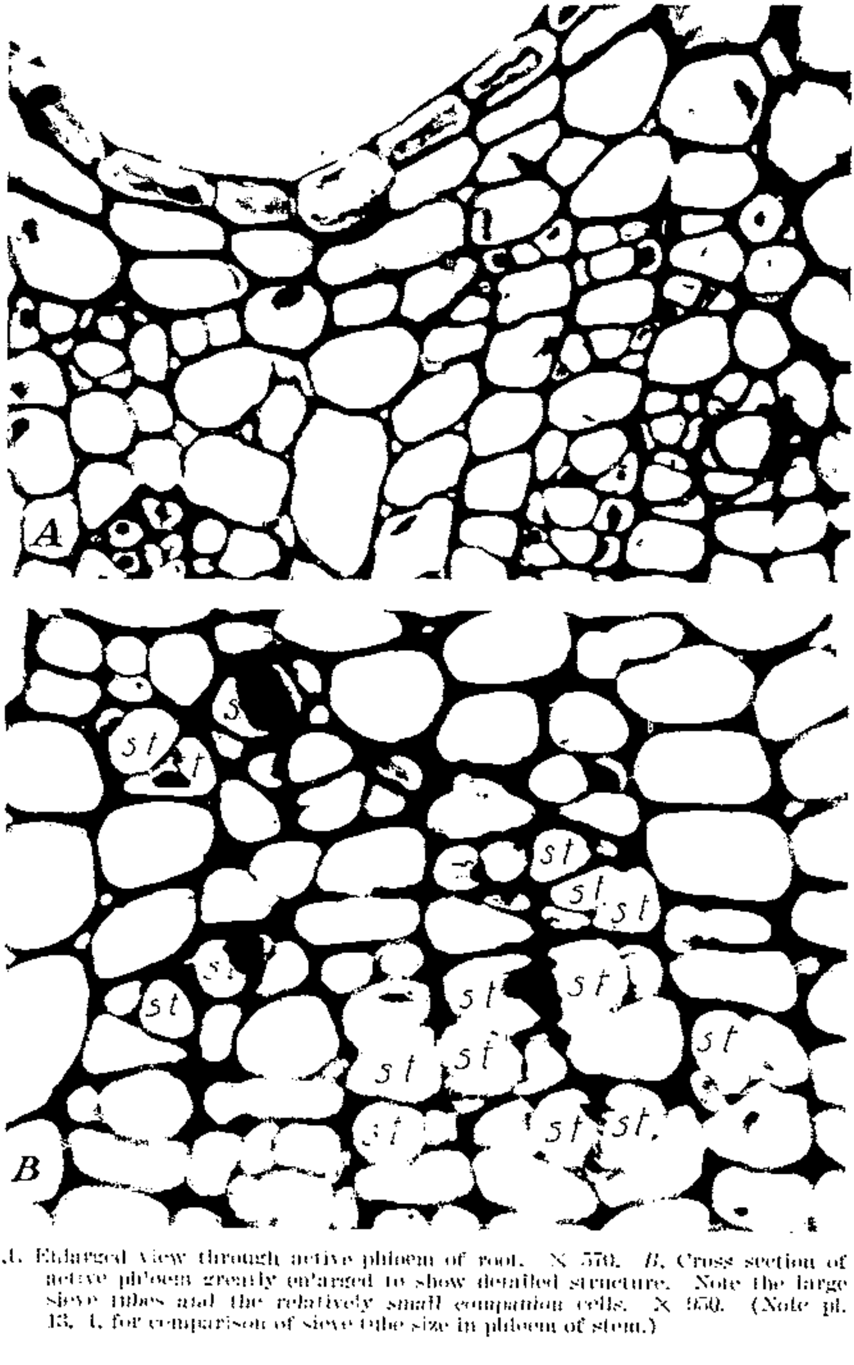
Cotyledon

The cotyledons are very small (3.5 mm. × 4.5 mm.), entire-margined and round or oval in outline (pl. 2, *A*). The petiole has a midrib and two laterals which, upon entering the lamina, branch profusely to form a complicated reticulum.

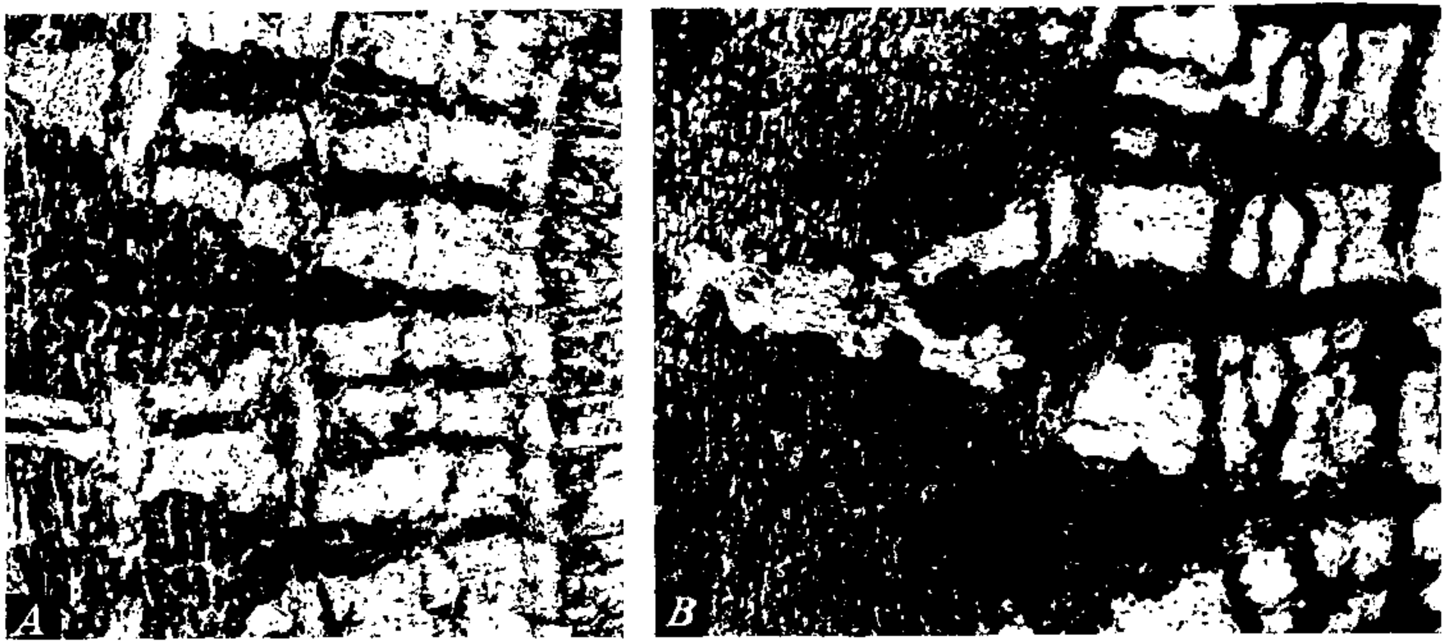
The mesophyll is composed of six layers of cells of which the upper two form the palisade region. The spongy cells adjacent to the palisade layer are frequently elongated to form a transition. Stomates are found on both surfaces, their frequency being slightly greater in the upper. There are no resin canals in the blade, and both the upper and the lower epidermis are free from hair.

True Leaf

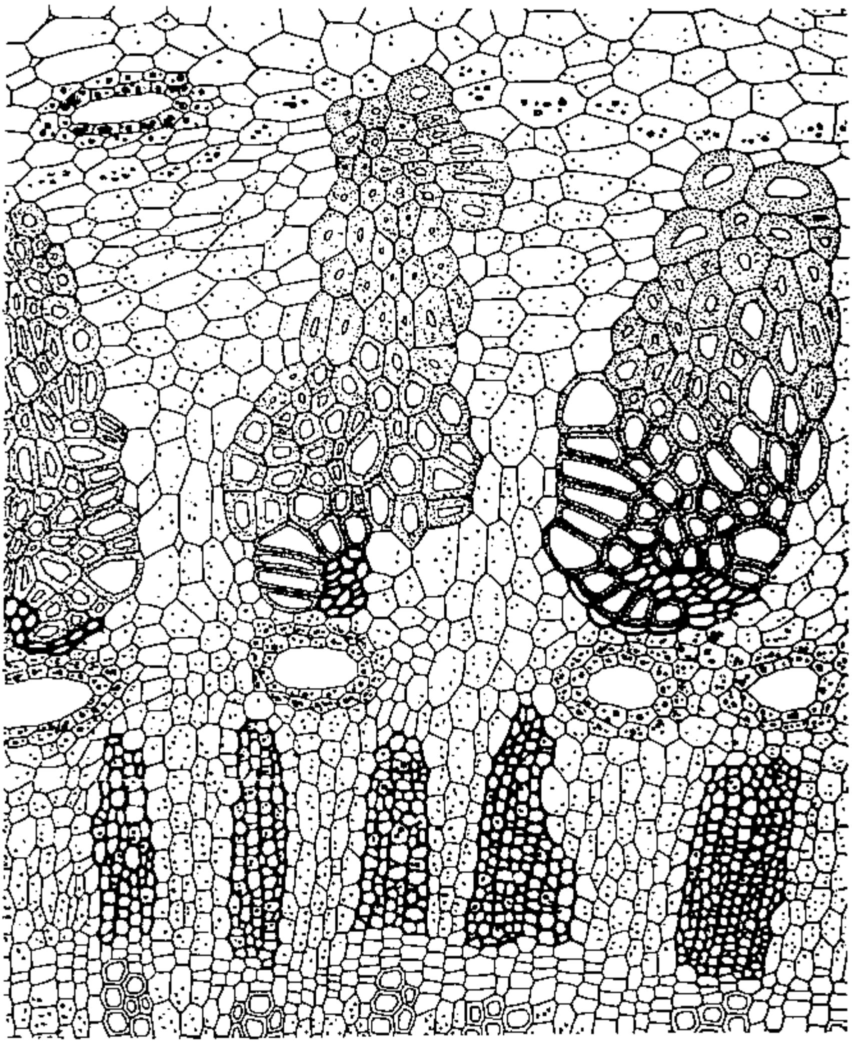
The gross morphology of the true leaves and the difference that exists between summer and winter leaves already have been pointed out. They are very variable in form; a few types are illustrated in figure 17, *A*.



A, Enlarged view through active phloem of root. × 570. *B*, Cross section of active phloem greatly enlarged to show detailed structure. Note the large sieve tubes and the relatively small companion cells. × 950. (Note pl. 13, *A*, for comparison of sieve tube size in phloem of stem.)



A, Section through the phloem of a branch (7.5 mm. thick) of Salinas strain No. 49, low in rubber. The plants were set out in 1930 and have never been irrigated. The slide was stained with Sudan III for rubber. Note the relatively small available storage space compared with figure at right. × 70. *B*, Section through the phloem of a branch (7.5 mm. thick) of Salinas strain No. 406, high in rubber. The plants were set out in 1935 and were irrigated once in 1941 and again in July 1942. The cortex is much broader than in *A*, and the storage space for rubber is larger. × 70. (Compare also *A* and *B* of pl. 23.)



Semidiagrammatic drawing of cross section of base of actively growing 4-month-old shoot. × 175. Orange color indicates rubber; blue color, starch.

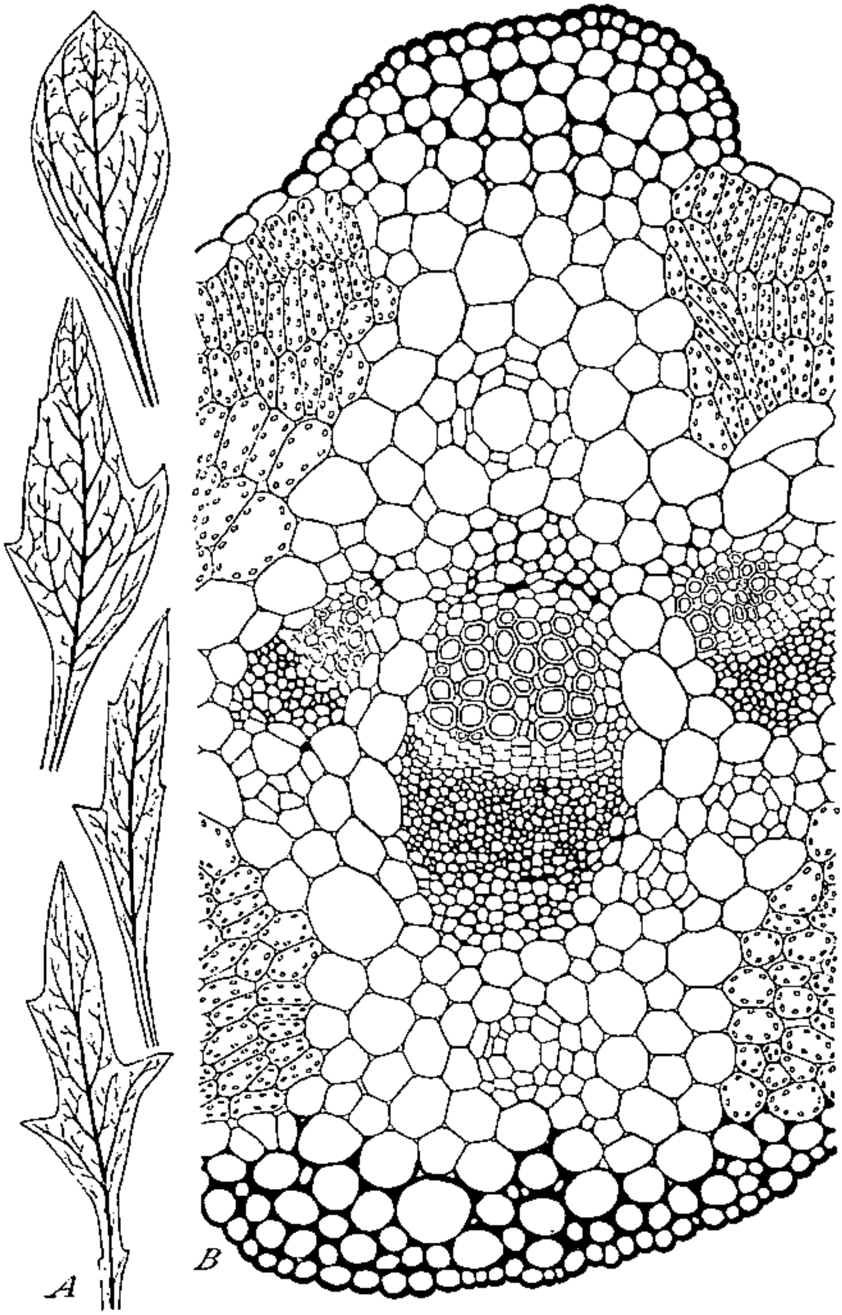


FIGURE 17.—A, Variation in types of summer leaves; B, cross section of midrib of leaf with dorsal and ventral resin canal. × 250.

Except in the region of the midrib, the lamina is thin (fig. 18, *A*). The epidermal cells in surface view are very sinuous (fig. 18, *C*); stomates are fairly abundant and occur with about equal frequency on both surfaces. The stomates are of the common type, somewhat depressed below the level of the epidermis, the walls of the guard cells slightly thickened in the region of the stomatal cavity. The

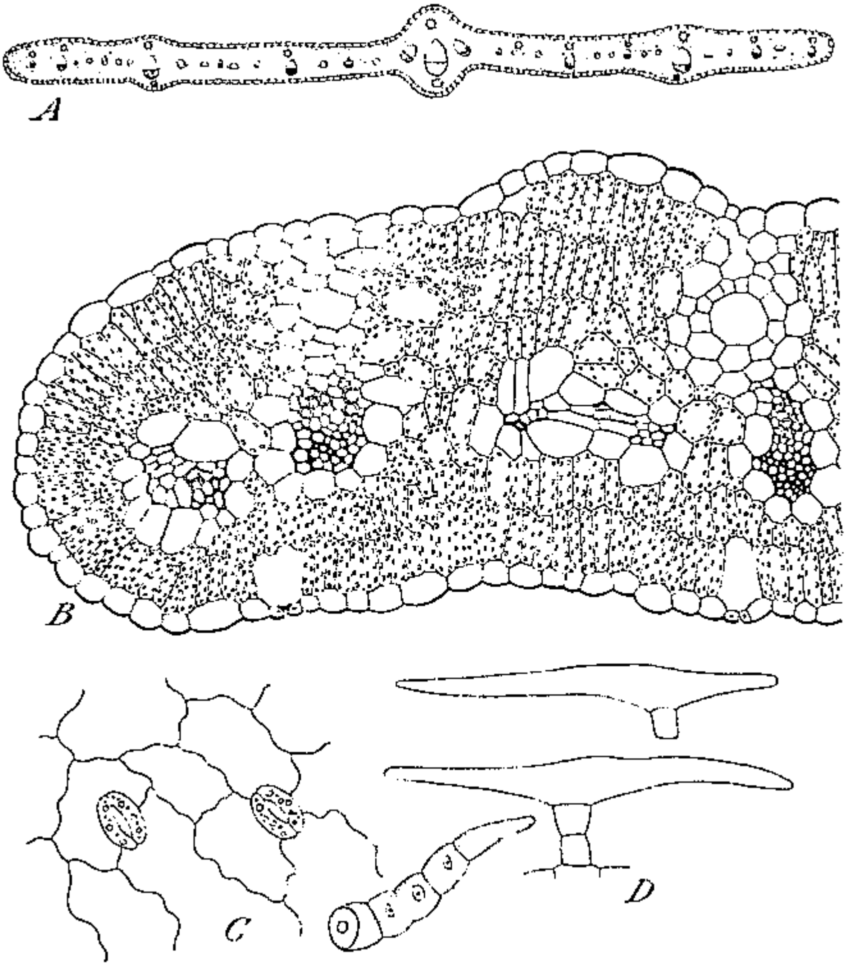


FIGURE 18.—*A*, Cross section of leaf; *B*, enlarged part of cross section to show detail in structure. × 100. *C*, Surface view of upper epidermis. × 200. *D*, Types of hairs. × 200.

mesophyll consists almost entirely of palisade cells equal in shape and distribution on both surfaces (fig. 18, *B*). Resin canals are found on both sides. There are 10 to 12 canals on the ventral or upper side and 4 to 5 on the dorsal, or lower. The dorsal canals accompany the leaf-trace bundles, but the ventral canals originate de novo in the petiole; here they follow the principal veins and give off side branches as they enter the basal region of the lamina.

There are two types of hairs found on either leaf surface. The more common type is the large, asymmetrical T-shaped hair (fig. 18, *D*) with a unicellular or bicellular stalk, which is so short that the hair appears sessile. Lloyd (*4*) describes and illustrates only T-shaped hairs with two- and even three-celled stalks; yet the one-celled stalk is very common. Much less frequently found is a small multicellular hair, the ultimate cell of which is long and slender.

ORIGIN AND STORAGE OF RUBBER

The occurrence of rubber and its centers of distribution in the various plant organs have been described in detail by Ross (*5*) and Lloyd (*4*). Rubber is found in all plant organs, but only the stem and the root have sufficient quantities to be of economic interest.

Generally speaking, in plants of harvest size the vascular rays of the phloem and, to a lesser extent, those of the xylem contain by far the largest amount of rubber (pl. 21, *A*, *B*). Smaller quantities are found in jacketing cells of the resin canals, and rather insignificant quantities in pith, primary cortex, and xylem parenchyma. The active sieve-tube tissue contains practically no rubber. The latter, though perhaps of some debatable significance in the economy of the plant, would have no value as stored rubber since the active phloem becomes in part obliterated and in part displaced by sclerenchymatous tissue.

In young plants in which the primary tissues are still a conspicuous part of the anatomical picture, most rubber is found in the primary cortex, pith, and vascular rays, as well as in the parenchymatous jacket of the primary resin canals.

In young, actively growing stems rubber appears first in the epithelial cells of the primary cortical and pith canals, but it is much more conspicuous in the secreting layer of the newly formed secondary resin canals. Small granules are also observed in the cells of the primary cortex, pith, and the inner cells of the rays (pl. 22). Of interest is the distribution of starch, which is limited to the endodermis and the layer of parenchyma cells sheathing the secreting layer of the resin canals (pl. 22). Sometimes starch is also observed in some of the parenchyma cells immediately inside the endodermis, between the groups of sclerenchyma fibers.

In old roots and stems that are composed mostly of secondary tissues, rubber secretion is related to the age of the cells as formed by the cambium. Since rubber normally appears first in older cells, except for the epithelium of the resin canals, the direction of rubber appearance will be for the phloem centrad and for the vascular rays of the wood, centrifugal. For the same reason, cells closer to the growing point of the plant axis will contain less rubber than will more basal cells.

The time factor for rubber synthesis and the duration of the rest period for maximum rubber storage will not be taken up in this bulletin. According to Lloyd (*4*)—

> the time at which the maximum amount of rubber may be expected differs with the length of the growing season, which depends upon the rainfall and the intensity of the drought following; the maximum quantity is certainly not reached in four months after growth commences, and it is highly probable that six or more months must elapse.

ANATOMICAL STRUCTURE IN RELATION TO RUBBER CONTENT AND TYPE

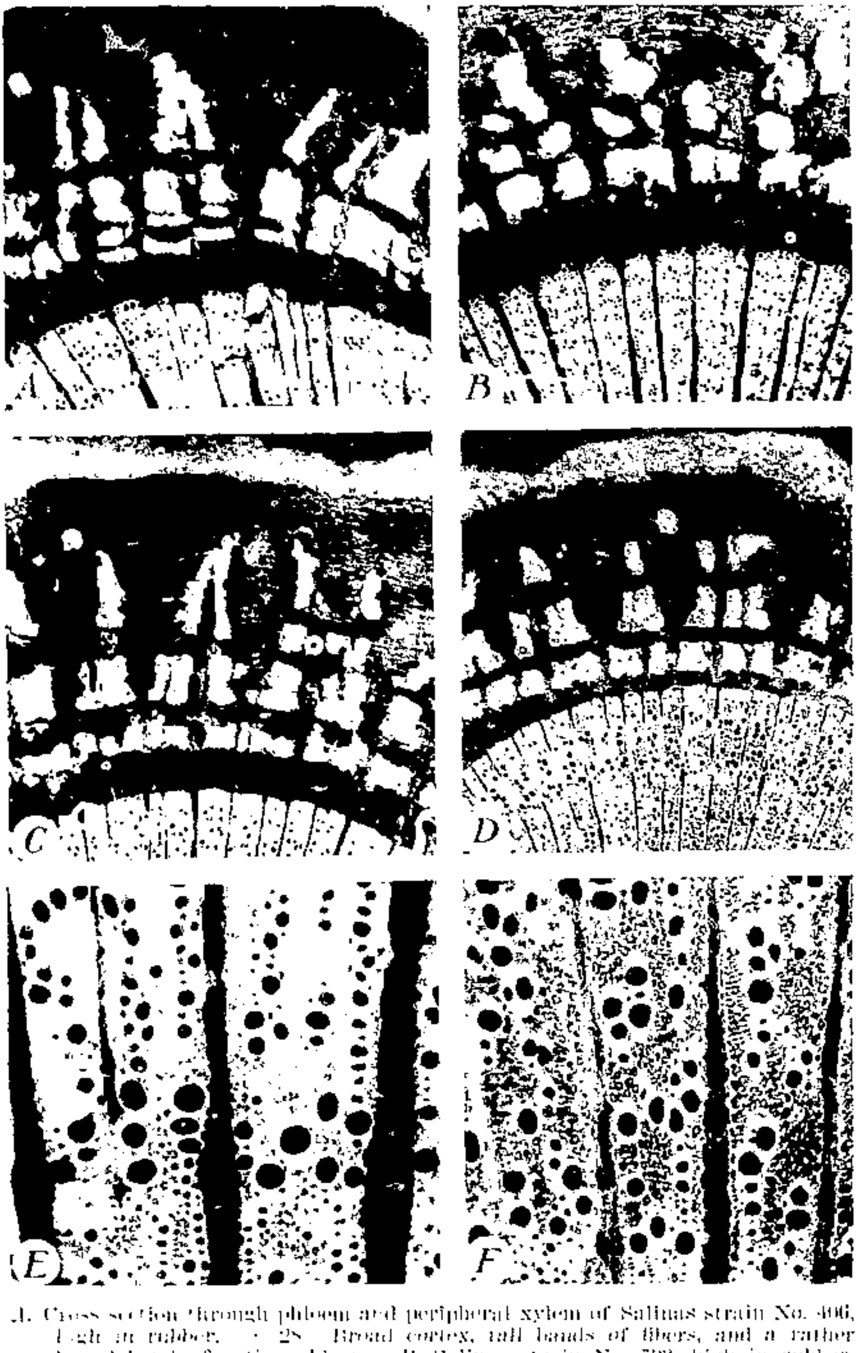
The rate of growth determines the total increment of xylem and phloem. According to Lloyd (*4*), more phloem is produced by dry-land plants than by plants under irrigation, but the sum total of rubber-storing tissue produced under irrigation is nevertheless greater, since the total growth increment is larger.

The effect of irrigation on structure also may find expression in the detailed anatomical picture of the wood itself. The xylem of irrigated plants, according to Lloyd, is harder, the vessels are smaller, and the mechanical elements are more compact. The vascular rays also are smaller, their cells thick-walled and lignified. Lloyd undoubtedly observed these differences, but unless observations are made with comparative material one may not generalize too freely. Varieties differ. These differences may be qualitative as well as quantitative (pl. 23, *A* to *F*). The relative size of cortex and wood appears to be a varietal characteristic that may not be affected by environment, although the total growth increment would be in direct relation to the amount of available water. Vessel size, as seen in cross section, also is apt to be a varietal characteristic and not an expression of available water. In one instance (pl. 23, *E*, *F*) the larger-size vessels were related to high rubber content, perhaps an accidental correlation, but in this case not a response of rate of growth to differences in water supply.

Very old plants may show lignification in the older part of the rays, but in plants of economic interest (4 to 5 years old) none of the material studied showed either increase in thickness of the ray cells or their lignification. Solitary or groups of pith cells do occasionally become thick-walled and lignified, a fact of rather minor importance.

As already stated in the introduction, it is necessary to know the varieties anatomically before attempting to interpret the effect of environment on structure. Since rubber storage appears to be related to structure, varieties with a greater storage space for rubber would furnish better raw material for selective breeding work than would varieties in which the secondary cortex is thin, even though both varieties might test high in percentage of rubber. The relative growth increments of xylem and phloem may also differ with different varieties. Only selections in which phloem development is favored over xylem should be afforded a future in a breeding program. Nothing is known about the "grand period" of cambium activity in the spring, although such a knowledge would have a definite influence on the date for the withholding of irrigation water to stimulate the synthesis of rubber. Again, in localities with a long growing season, definite data on the length of the rest period for maximum rubber synthesis would permit a second period of active growth before cell division is suspended with the advent of winter.

The anatomical approach in an improvement program for guayule has much to recommend itself: it affords a scientific basis for purposeful selection and points to short cuts in the attainment of this goal.



A, Cross section through phloem and peripheral xylem of Salinas strain No. 406, high in rubber. × 28. Broad cortex, tall bands of fibers, and a rather broad band of active phloem. *B*, Salinas strain No. 593, high in rubber. Planted in the field in 1941 and irrigated the same year and in July 1942. × 28. Compared with *A* the cortex is narrow and the sclerenchyma groups rather broad. The zone of active phloem is broader than in *A*. Xylem rays

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are somewhat farther apart. *C*, Salinas strain No. 406, high in rubber. × 28. Set out in 1935 and never irrigated. *A* and *C* are very similar in appearance (being the same strain) and irrigation does not seem to have had any effect on the structure. *D*, Salinas strain No. 49, low in rubber. Set out in 1930 and never irrigated. × 28. The cortex is narrow, and the available storage space for rubber is not as great as in *A* and *C* but just as great as in *B*. The difference between *B* and *D* seems to be the relatively narrow band of active phloem in *D* as compared with the broad band in *B*. *E*. Enlarged view of xylem and vascular rays of strain No. 406 (not irrigated). × 180. *F*. Enlarged view of xylem of strain 49. × 180. Note the larger vessels and wider rays in strain No. 406 compared with those of strain No. 49.

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