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Wild Morning-Glory or Field Bindweed

P. B. KENNEDY AND A. S. CRAFTS

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## THE ANATOMY OF CONVULVULUS ARVENSIS, WILD MORNING-GLORY OR FIELD BINDWEED

P. B. KENNEDY<sup>1</sup> AND A. S. CRAFTS<sup>2</sup>

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### INTRODUCTION

No one familiar with the economics of agriculture can doubt the importance of weed control, yet very little fundamental research has been published in connection with this problem. The intelligent use of cultural practices or chemical agents depends upon a knowledge of the anatomy and physiology of the weed concerned, especially if it is a perennial. The present paper is an attempt to describe those phases of the anatomy of morning-glory which form the background for a physiological study which it is hoped will result in the development of a basic method of control.

### GROWTH HABITS

The morning-glory plant, if subjected to varying environmental conditions, occurs in a number of forms. Variation in size and form of the leaves and stems is usually associated with the supply of moisture, but may also result from frequent cutting, which tends to deplete the food reserves in the root. The form of development taken by the root system is frequently related to the soil type and water table. The taproot being primarily a storage organ, a large proportion of the tissue is alive and respiring. This necessitates an oxygen supply during the growing season, and it will be found that all old roots are

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of such a form that only the current season's growth actually penetrates below the summer water level. Consequently, in localities where there is a high water table, the taproot may branch at a depth of 2 feet or less, while in other localities, it may penetrate to a depth of 10 feet or more before branching profusely.

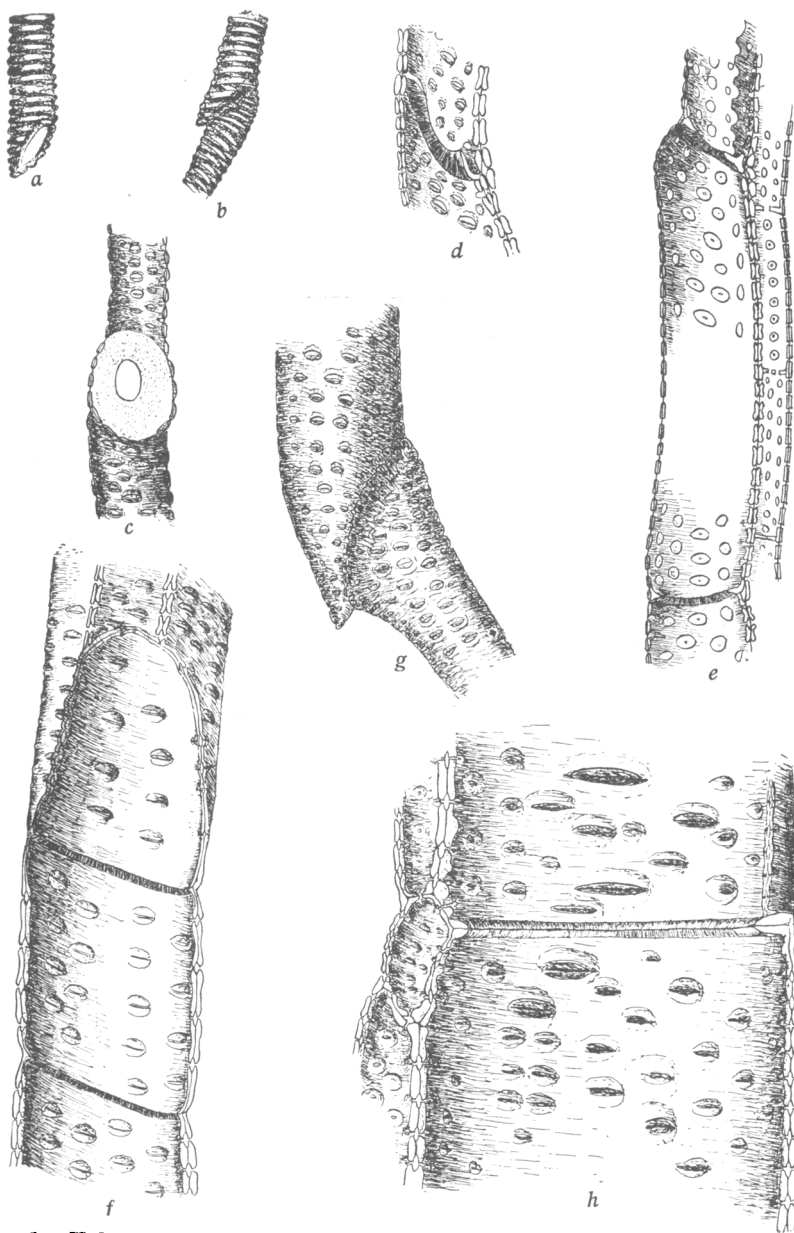
The root system of this plant is characterized by the production of annual laterals in great numbers. These laterals develop adventitiously throughout the length of the taproot and its branches, and permeate the soil in all directions. Most of them die at the end of the season and are replaced by new ones each year; but any which have become favorably situated may make more than average growth and become so well developed that they persist as permanent branches. It is by means of these persistent laterals that spreading in a horizontal direction is accomplished. Shoot buds arise on these horizontal laterals and develop into rhizomes which, reaching the surface, establish new crowns.

The unusual ability of the morning-glory plant to reproduce vegetatively is related to the form of its underground structures. The relatively large storage capacity of the root necessitates the existence of many living cells in close relation with a large supply of food, and an efficient system for absorbing mineral nutrients. These conditions favor bud formation, which is the most characteristic habit of the plant (fig. 27, page 621). Favorable growing conditions stimulate intense activity, and these buds may be produced by dozens or even hundreds (fig. 22, page 616), especially during warm weather and after a cultivation which has destroyed the top growth. The ability to produce buds, together with the food reserve of the root, favors vegetative reproduction and makes the plant persistent. The dense foliage and twining growth enable the plant to choke out competitors and present difficulties to thorough spraying.

## GROWTH AND STRUCTURE

*Primary Development in the Stem.*—When the seed of morning-glory germinates, the developing shoot pushes out from between the expanding cotyledons and initiates the growth of those structures which constitute the primary stem. Protoxylem elements differentiating from the procambial strands form isolated rays of annular and spiral vessels roughly corresponding to the phyllotaxy of the species. These vessels, composed of elongated cells with almost completely dissolved end walls (fig. 1) range from 0.010 mm. to 0.025 mm. in diameter.





**Fig. 1.** Xylem vessels showing dissolution of end walls (X500).

- A*, Spiral element of stem protoxylem.
- B*, Conjunction of two spiral elements in the stem.
- C*, Pore in end wall, metaxylem of stem.
- D*, Side view of *C*.
- E*, Metaxylem vessel of stem.
- F*, Secondary xylem vessel of the stem.
- G*, Conjunction of two xylem vessels at junction of branch with main stem.
- H*, Secondary xylem vessel of the root.



The groups of protoxylem strands (fig. 2) are limited on the inner side by protophloem and on the outer side by procambium tissue followed by external protophloem (fig. 2); thus bicollateral bundles occur in this stem. The protoxylem strands consist of two or three tubes resulting from centrifugal growth. The bundles into which these endarch strands are grouped are roughly separated by rays of pith parenchyma. Rarely do these rays completely dissect the internal

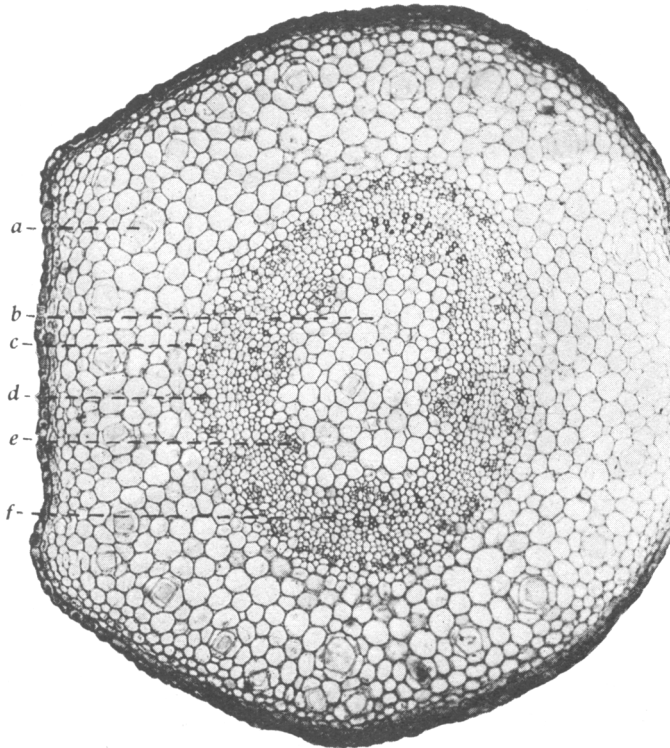


Fig. 2. Transverse section showing primary stem structure (X94). *a*, Latex vessel; *b*, pith; *c*, starch sheath; *d*, external phloem; *e*, internal phloem; *f*, primary xylem. The bundles of phloem and xylem in this figure include protophloem and metaphloem, and protoxylem and metaxylem.

phloem; they merely throw it into groups on the inside of the vascular cylinder (fig. 2). Metaxylem elements formed on the outer edges of the protoxylem strands increase in size in successive layers, ranging from 0.025 mm. to 0.060 mm. in diameter. The broadening xylem strands approach each other at the sides until they are separated only by xylem rays differentiated from the procambium, and soon these strands merge to form a complete cylinder (fig. 3).



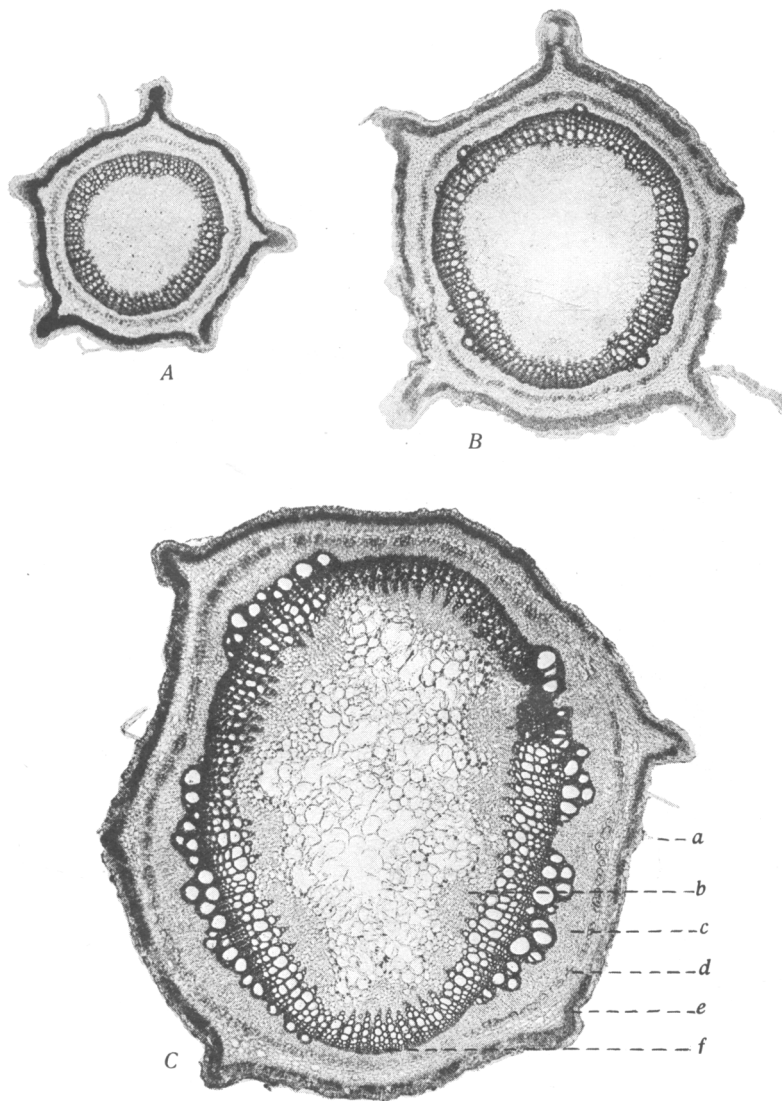


Fig. 3. Transverse sections of stem (X25).

*A*, Near the outer end.

*B*, Median portion; no branching from leaf axils.

*C*, Near crown. Three branches from leaf axils occurred between *B* and *C*. *a*, clothing hair; *b*, internal phloem; *c*, external phloem; *d*, pericyclic fibers; *e*, chlorenchyma; *f*, secondary xylem.

The internal phloem rapidly approaches its mature form. The external primary phloem increases slightly during differentiation, but most of the phloem of the mature stem is secondary. The pericycle, consisting of one or two layers of parenchyma cells during primary development, differentiates into an encircling sheath of thick-walled fibers as secondary growth is initiated (fig. 3, *B* and *C*).

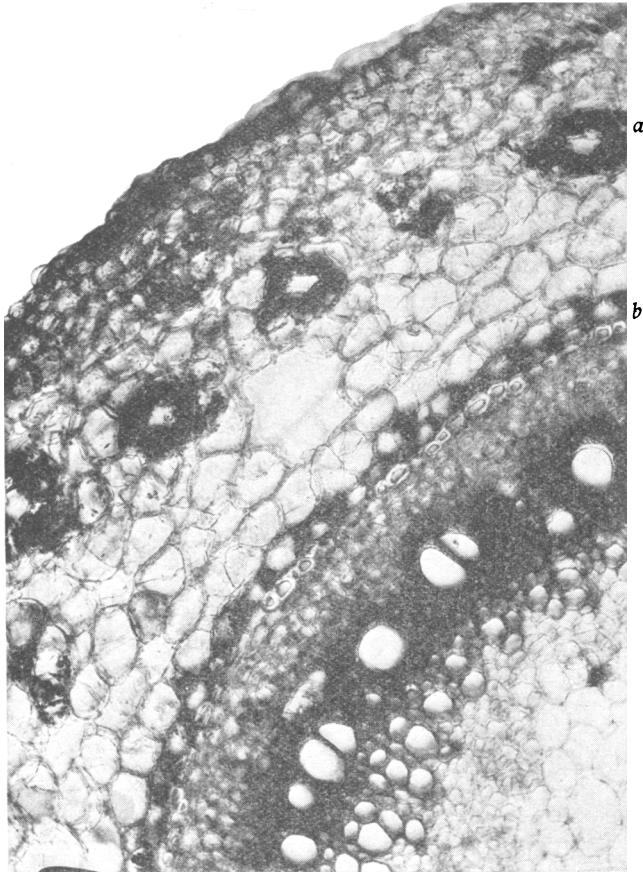


Fig. 4. Transverse hand section of rhizome showing starch in the cells which surround the latex vessels and in the starch sheath. Stained with I.K.I. (X130.) *a*, Latex vessel; *b*, starch sheath.

The starch sheath or endodermis contains small green-colored starch grains (fig. 4) throughout the development of the primary stem, but these are later lost. They gravitate to the bottoms of the cells and correspond to the statoliths mentioned by Haberlandt.<sup>(1)</sup>

The cortex is a broad band consisting of undifferentiated parenchyma surrounding the starch sheath, scattered latex vessels, and two or three layers of chlorenchyma cells. A single layer of cells with a thin cuticle forms the epidermis.

Latex vessels occur abundantly in the cortex and pith of the stem. Each vessel consists of a column of cells with the end walls partly dissolved and is closely surrounded by a uniseriate layer of small cells densely filled with protoplasm. The vessels are heavily pitted, and although no starch occurs in the latex, the surrounding cells are usually well stored with it (fig. 4).

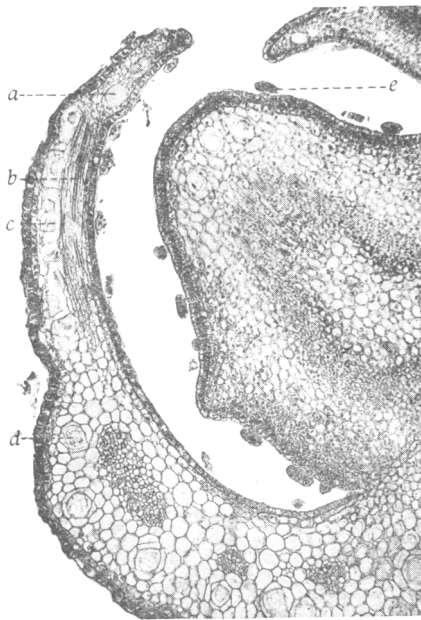


Fig. 5. Transverse section of shoot tip showing secretory cells in relation to vascular tissues in the very young leaf (X80). Note longitudinal view of vein and accompanying secretory cells. *a*, Latex vessel breaking down to form an air pocket; *b*, leaf vein in longitudinal section; *c*, latex vessel in longitudinal section; *d*, latex vessel in transverse section; *e*, glandular hair.

Hairs of two types occur on the young stem: clothing hairs, each consisting of a short basal cell and a long terminal cell (fig. 3, *A* and *C*); and glandular hairs, each made up of a small compact group of cells, about eight in number, mounted on a single basal cell (fig. 5). These glandular hairs occur in small indentations in the epidermis and are inconspicuous on the living plant. Their dense cytoplasm and large nuclei stain deeply, making them prominent in stained preparations of young tissues.



*Secondary Development in the Stem.*—Closely following the maturity of the metaxylem, certain parenchyma cells at the outer extremities of the primary xylem strands resume meristematic activity and, at about the time the xylem cylinder has become closed, a cambium layer is established and secondary growth starts. The stem and leaves have developed meanwhile to approximately mature form; transpiration is high and growth conditions optimum. Normally the first few layers of secondary vessels attain the greatest diameter of any in the stem, measurements of 0.075 mm. having been recorded. They are well fitted for rapid conduction, the end walls being practically eliminated by dissolution (fig. 1 *F*). After about two layers of these highly-specialized tubes are formed, development slows down, surfaces are more highly cutinized, reproductive activities call upon the resources of the plant and meristematic activity becomes less pronounced (fig. 3 *C*). There is a gradual decrease in the size of the xylem elements until at the end of the normal growing period of the stem an 'annual ring' of small, thick-walled, heavily lignified wood elements is formed which materially strengthens the stem but adds little to its conductive capacity (fig. 3 *B*). The arrangement of the xylem vessels in the form of strands separated by rays of living wood parenchyma continues throughout secondary growth of the stem.

Cambial activity also results in the production of secondary phloem composed of sieve tubes, companion cells, and phloem parenchyma. No fibers occur in this tissue (fig. 6).

The pericyclic fibers thicken and form a distinct mechanical layer around the vascular cylinder. Vestiges of an internal ring of pericyclic fibers may be found in many stems but it is never well developed.

The cortical cells become more or less flattened, owing to growth from within, but no breaking down of tissues occurs during the normal life of the stem. The latex vessels in the cortex and pith remain open and active as long as the stem is alive.

The epidermis of the stem becomes heavily cutinized and the cuticle has a peculiar form, being very finely corrugated on the outer surface in a longitudinal direction. These fine ridges and furrows on the stem, the uneven surface of the leaves, and the clothing hairs in the young tissue, make this plant difficult to wet, an important factor in control by the spray method.

*The Leaf and Petiole.*—The leaves are formed early in the ontogeny of the stems (fig. 5). The tracheal system in the young leaf (fig. 7) is composed of spiral protoxylem elements ranging from 0.007 mm. to 0.014 mm. in diameter, with a mean value of about 0.01 mm. It

develops concurrently with the xylem of the stem. Only protoxylem strands extend from the stem into the petiole. At the base of the petiole, the leaf trace divides into one main central bundle and four

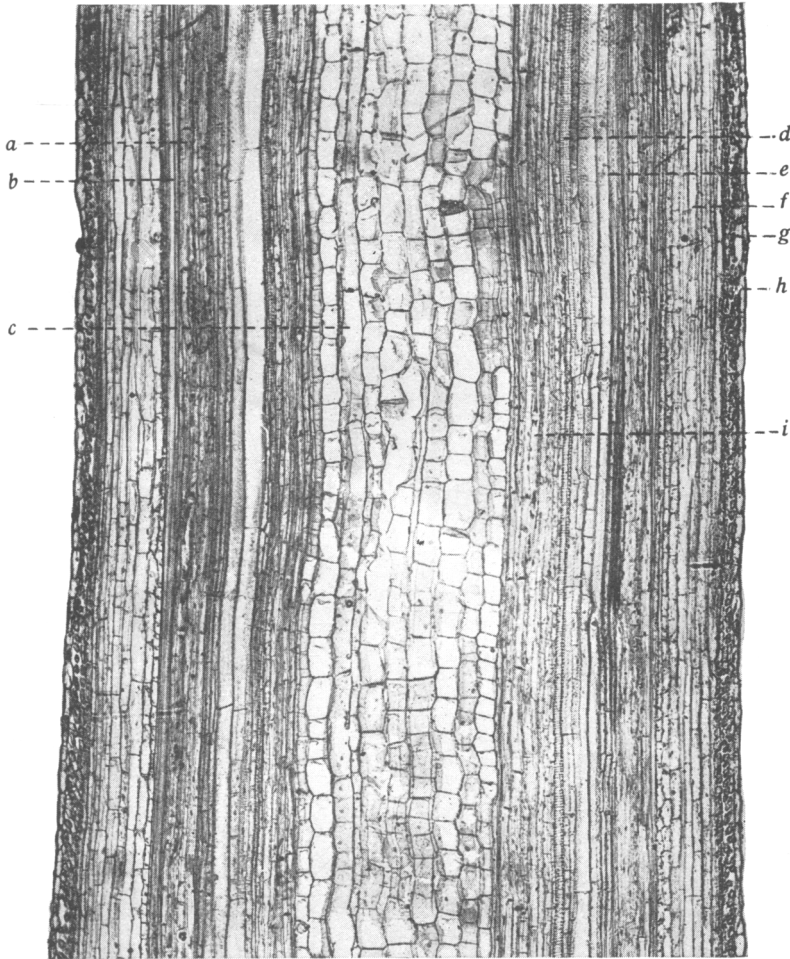


Fig. 6. Longitudinal section of the stem (X50). Primary and secondary xylem tissues are well illustrated. Sieve tubes may be found in both external and internal phloem. Tissue relationships are brought out by a comparison with figure 3. *a*, Sieve tube of external phloem; *b*, pericyclic fiber; *c*, latex vessel in pith; *d*, primary xylem; *e*, secondary xylem; *f*, cortex; *g*, chlorenchyma; *h*, epidermis; *i*, sieve tube of internal phloem.

small lateral bundles. These remain distinct throughout the petiole, but branch as they enter the leaf blade. Petit<sup>(2)</sup> has used the number of bundles in the petiole as a differentiating character to distinguish



Fig. 7. Cleared leaf showing distribution of xylem tissues (X22).  
a, Primary xylem elements in leaf.



*Convolvulus arvensis* from *C. sepium*. The main or central bundle of the petiole is bicollateral and the xylem is entirely of protoxylem (fig. 8), the tracheal tubes ranging in size from 0.010 mm. to 0.025 mm. The four small lateral bundles are collateral, with the xylem on the ventral side. At the base of the leaf blade, the main bundle gives rise



Fig. 8. Cross section of petiole (X90), showing primary vascular tissues. *a*, Lateral bundles; *b*, chlorenchyma cells; *c*, main bundle (bicollateral); *d*, latex vessel (dorsal side).

to several branches, and these, with the lateral subdivisions of the midrib, form a network of tubes in the leaf (fig. 7). These branches, or veins, remain bicollateral for a short distance; but the phloem on the ventral side is soon reduced, leaving the bundle collateral. The latex vessels arise in the mesophyll tissue on the dorsal side, and may

be found paralleling all of the larger veins in the mature leaf (figs. 9 and 10). The xylem of the veins divides and redivides, until at the terminals of the bundles, three, or two, or even a single tracheid, may be found. The phloem is reduced more rapidly in the smaller bundles,

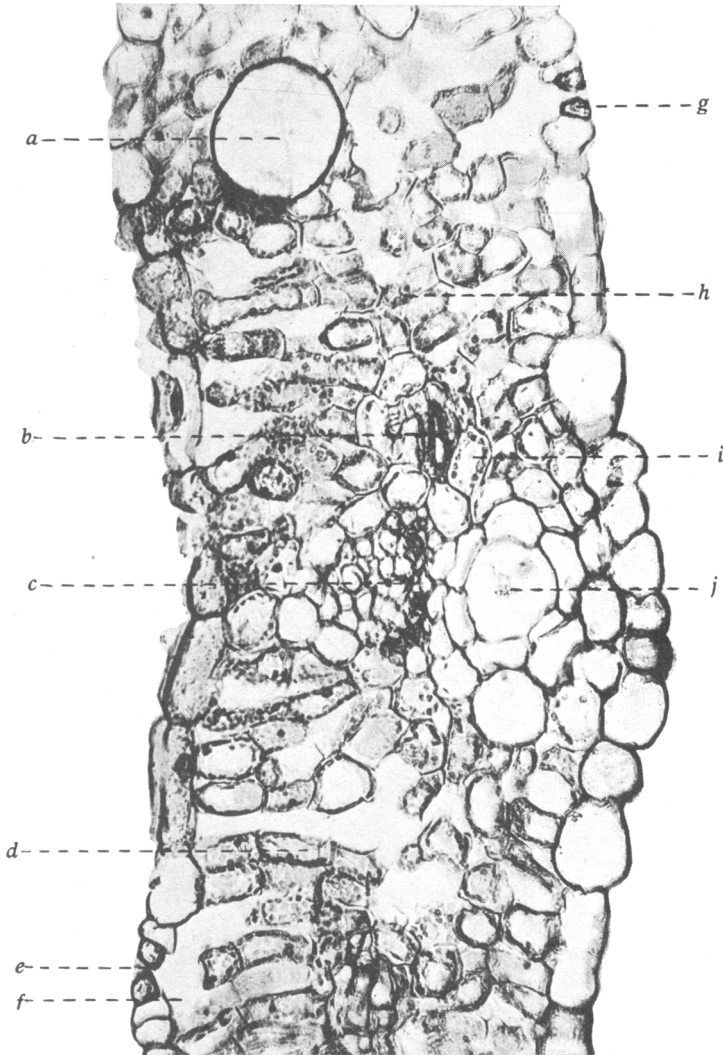


Fig. 9. The leaf (X265). The latex vessel is on the dorsal side of the vascular bundle. The air pockets are separated from the stomatal chambers by thick walls. *a*, Air pocket; *b*, terminal bundle; *c*, vein; *d*, palisade cells; *e*, stoma; *f*, stomatal chamber; *g*, guard cell; *h*, spongy parenchyma; *i*, transfusion cells; *j*, latex vessel.

and gives way to parenchyma at the terminals. The bundle ends are surrounded with transfusion parenchyma, so that in no place are the tracheids exposed to the atmosphere. The bundles in the leaf divide and anastomose, forming definite islets (fig. 7).

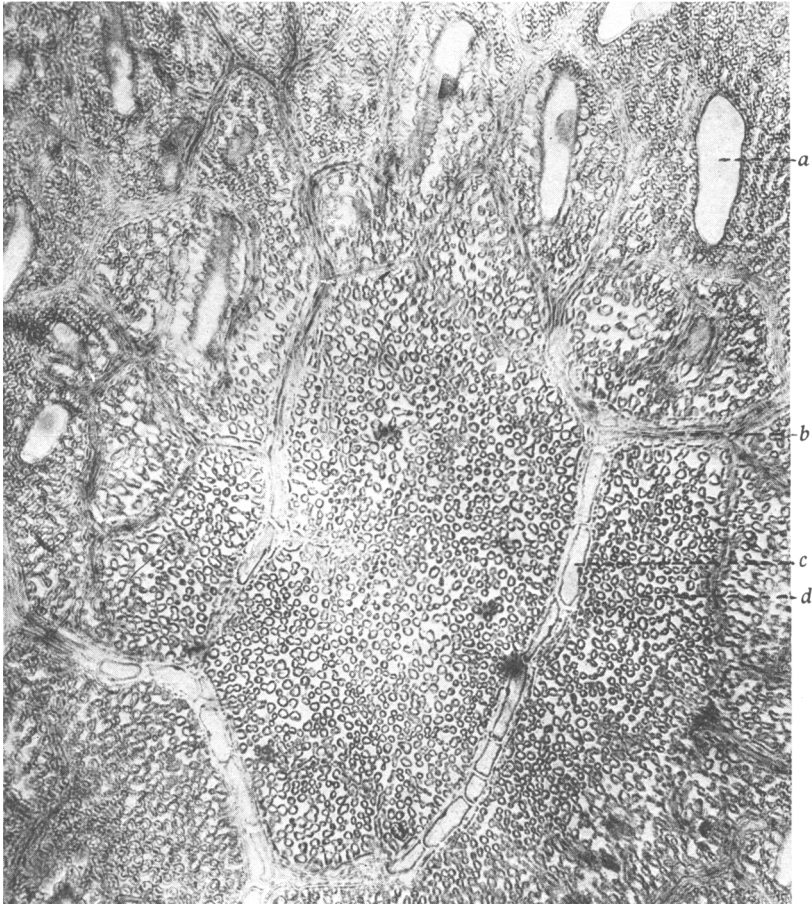


Fig. 10. Leaf structure showing relationship of latex vessels and air pockets to vascular and mesophyll tissues (X90). *a*, Air pocket; *b*, vein; *c*, latex vessel; *d*, palisade cells.

Situated in the mesophyll, at approximately the center of nearly every islet, and lying about equidistant from the upper and lower leaf surfaces, are air pockets (figs. 9 and 10). These are distinct from the normal air chambers of the leaf and are separated from them by a definite wall. They are apparently formed from those latex vessels which, lying between the veins, cease functioning as the leaf develops,



and become constricted by the developing vascular tissues, ultimately becoming isolated (fig. 5). After this, the breaking down of all internal walls results in an ovoid cavity, the contents of which are displaced by air (fig. 10).

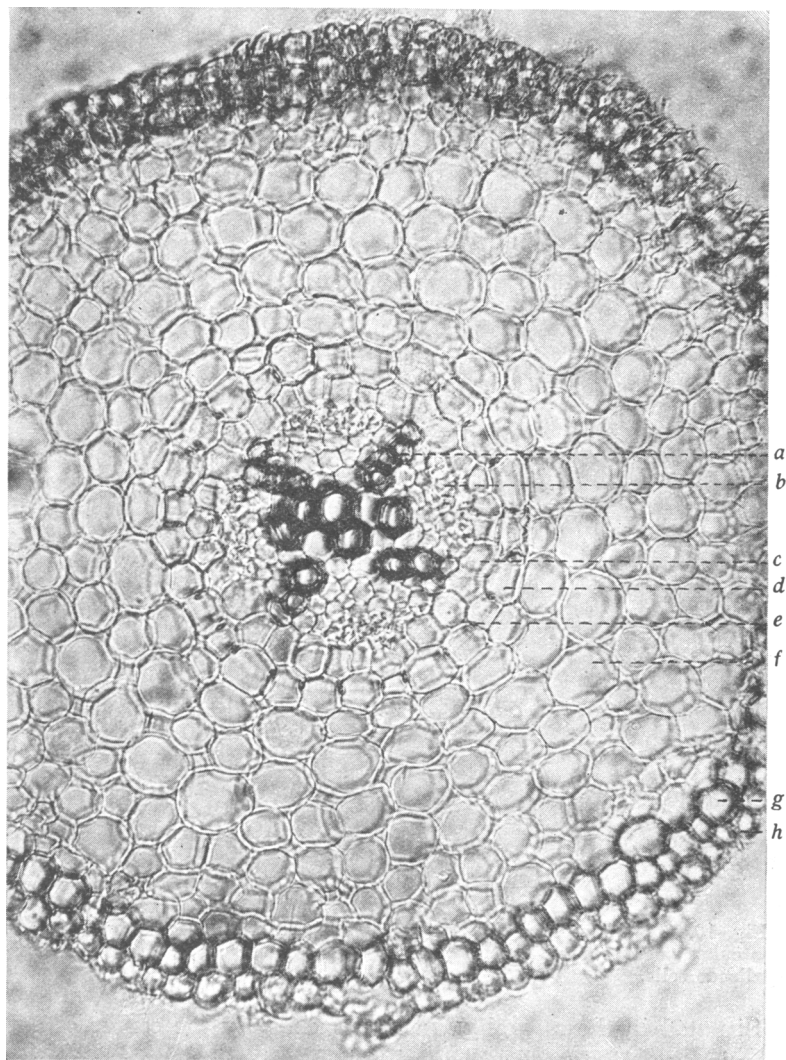


Fig. 11. Transverse section of a primary root showing radial arrangement of the vascular tissues, pericycle, endodermis with casparian strips, cortex, and epidermis. Free-hand section stained with phloroglucinol and hydrochloric acid (X275). *a*, Radial primary xylem strand; *b*, primary phloem; *c*, pericycle; *d*, endodermis; *e*, casparian strip; *f*, cortex; *g*, hypodermis; *h*, epidermis.

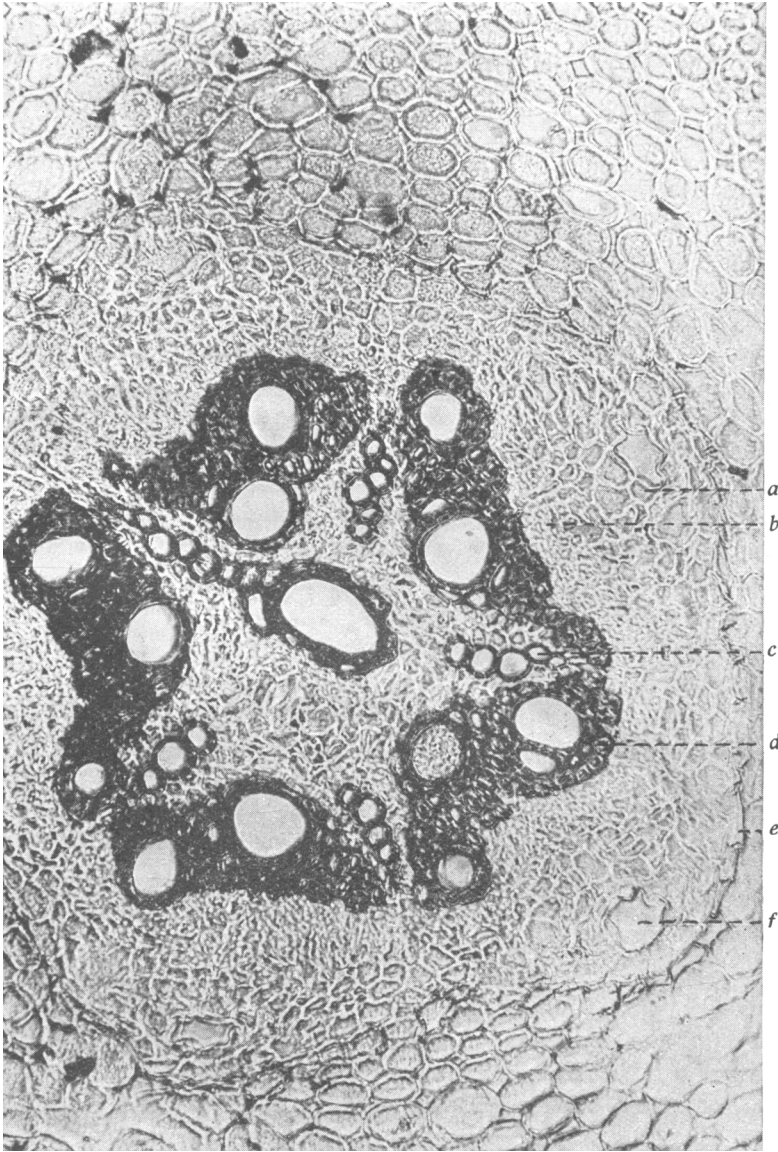


Fig. 12. Young root (X160). The primary xylem strands show radial arrangement. The endodermis is being stretched and the large latex vessels of the primary phloem collapsed by the internal pressure resulting from secondary growth. *a*, Primary phloem; *b*, secondary phloem; *c*, primary xylem strand; *d*, secondary xylem; *e*, endodermis; *f*, latex vessel.

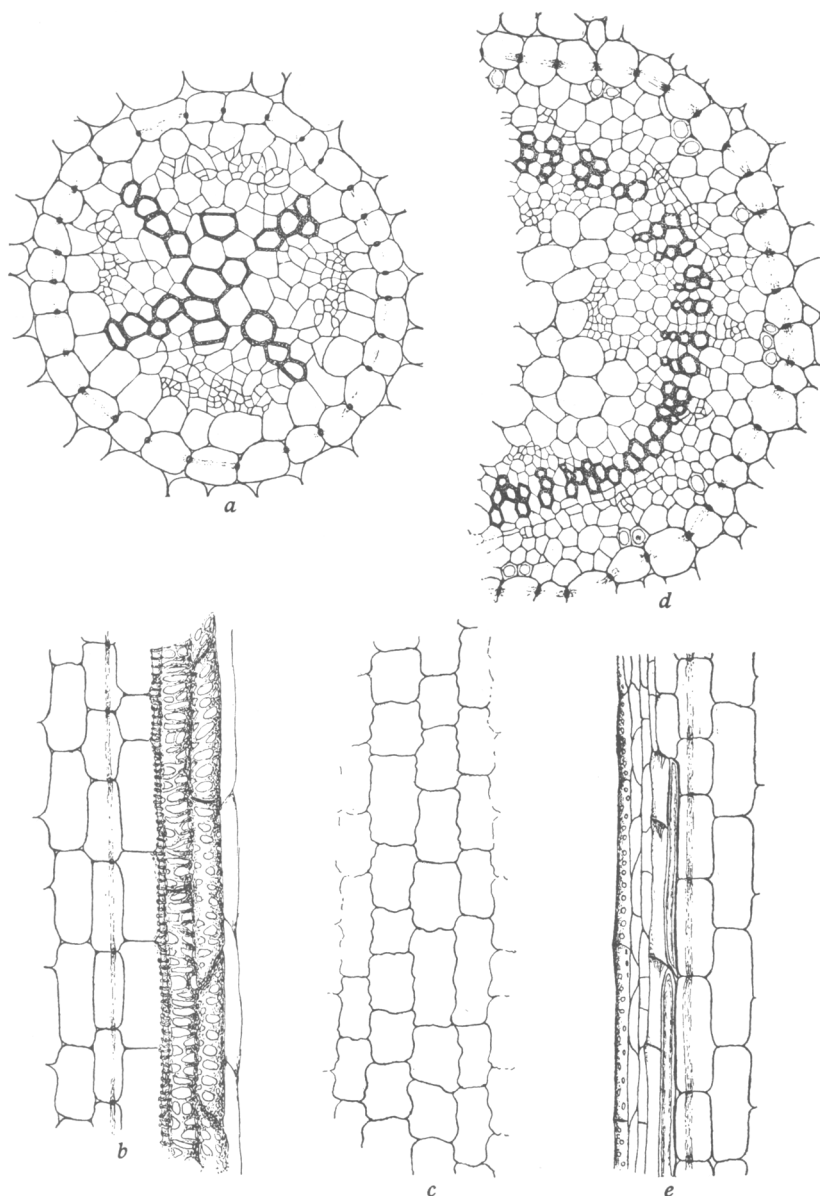
The mesophyll of the leaf is composed of two types of cells. Spongy parenchyma, composed of isodiametric cells with large intercellular spaces, surrounds the vascular system and air pockets, forming an air-chamber system which reaches to the stomata. Palisade parenchyma forms a double layer between the epidermis and the spongy parenchyma on both the dorsal and ventral sides. The differentiation between palisade and spongy cells is not so pronounced in the morning-glory leaf as in the leaves of many plants, and the double layers are not distinct, the inner one on the dorsal side being irregular (fig. 9).

The epidermis of the leaf is simple, and the cells are irregular in size and contour, giving the surface of the leaf a rough appearance similar to that of cobblestone pavement (fig. 9). The cells are thin-walled and not heavily cutinized. Stomata are present on both leaf surfaces, about 30 per sq. mm. on the ventral surface and about 45 per sq. mm. on the dorsal surface.

*Primary Development in the Root.*—As is the case with the great majority of roots, the root of morning-glory has a radial arrangement of its vascular tissues (fig. 11). The xylem, in most cases, is pentarch (fig. 12), development being centripetal. The only spiral elements are the first-formed tubes at the outer tips of the primary xylem strands. These range in size, with those of the stem, from 0.01 mm. to 0.025 mm. in diameter. On the inside of these are one or two columns of scalariform elements. These radial xylem strands are surrounded by parenchymatous tissue, which varies in amount in different roots. Typical pith is scant or wanting in the true root. Between the xylem strands lie groups of primary phloem (fig. 11), well differentiated from the surrounding parenchyma cells.

The latex vessels of the root occur mostly in the phloem, those in the cortex functioning only during the first few years. In the primary phloem, they occur in a group, usually one large tube surrounded by a few smaller ones (fig. 12). The presence of latex in the phloem of the primary roots proves the presence of latex tubes, and, by careful observation, these may be found after differentiation has been completed. An abundance of latex may be seen flowing from roots, especially if they are cut under water with the tops remaining intact.

The pericycle consists of a single layer of large parenchyma cells. The endodermis is made up of thin-walled cells intermediate in size between those of the pericycle and cortex (fig. 11). The casparian strip is very distinct in this endodermis, especially in water-culture roots which have been growing slowly (fig. 13).



**Fig. 13.** Endodermis of young root and rhizome.

- A*, Transverse section of primary root showing vascular tissues, pericycle, and endodermis (X250).
- B*, Radial section of the same tissues (X250).
- C*, Tangential section through the endodermis of the same root showing the nature of the casparian strips (X250).
- D*, Transverse section of young rhizome at time of cambium initiation showing formation of pericyclic fibers and casparian strips in the endodermis (X200).
- E*, Radial view of the same tissues (X200).



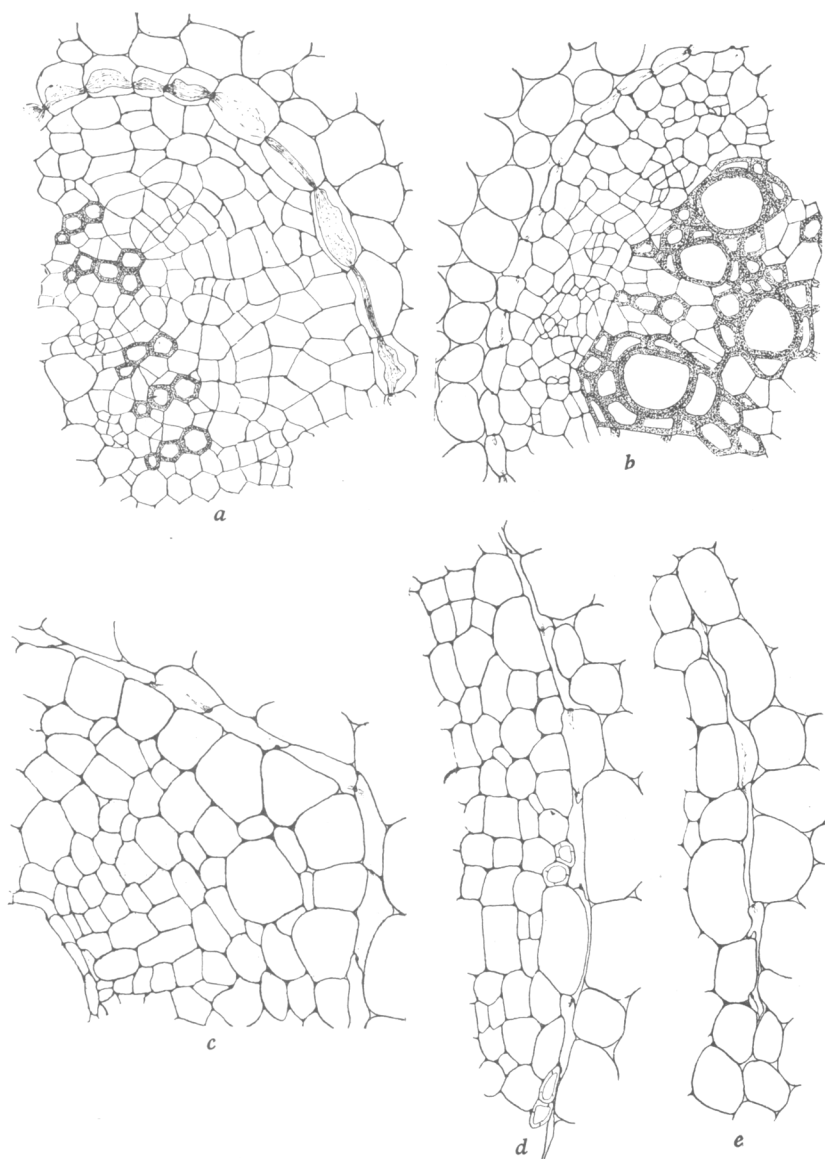


Fig. 14. Destruction of the endodermis.

*A*, Plasmolyzed transverse section of young rhizome showing relation of protoplast to casparian strips (X250).

*B*, Endodermis of young roots after secondary growth has started (X200).

*C*, Endodermis being stretched in one-year-old root (X250).

*D*, Further stretching as shown in a three-year-old rhizome (X150).

*E*, Fragment of endodermis in the cortical tissues of an old root (X150).

The cortex is composed of large parenchyma cells with prominent intercellular spaces. Latex tubes may be distinguished by the particular grouping of the immediately surrounding layer of cells. The outer cortical layer is slightly cutinized forming a hypodermal layer; outside of this is the epidermis proper (fig. 11). Under ordinary soil

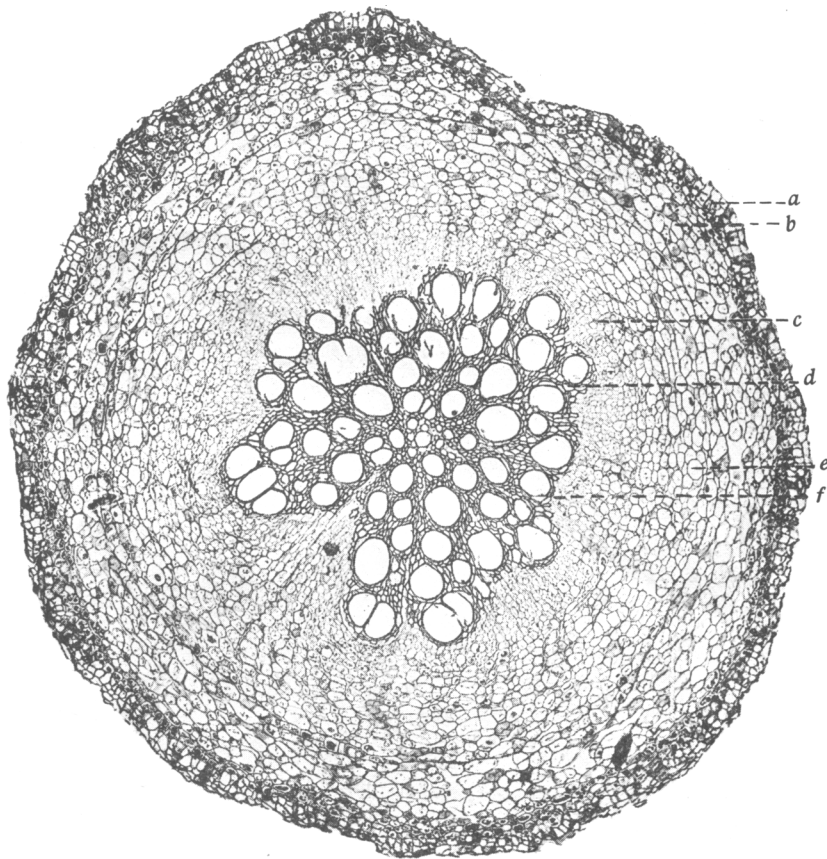


Fig. 15. Transverse section of the root (X35). Conduction of water and storage of starch are the chief functions of the secondary root. *a*, Phelloderm; *b*, cortex; *c*, secondary phloem; *d*, secondary xylem; *e*, latex vessel; *f*, cambium.

conditions, root hairs are formed in abundance from the epidermal cells, but plants growing in water culture fail to develop root hairs, a phenomenon common to many plants.

*Secondary Development in the Root.*—Following rapidly upon the primary development of the root, cambial activity is initiated in the angles between the xylem strands, and secondary growth starts. The

angles are soon filled with secondary xylem, the primary phloem being displaced and crushed by the internal pressure (fig. 12). When the secondary growth reaches the outer extremities of the primary xylem strands, the cambium forms a complete ring, not, however, becoming a perfect cylinder, but lying in an undulating band around the xylem (fig. 15).

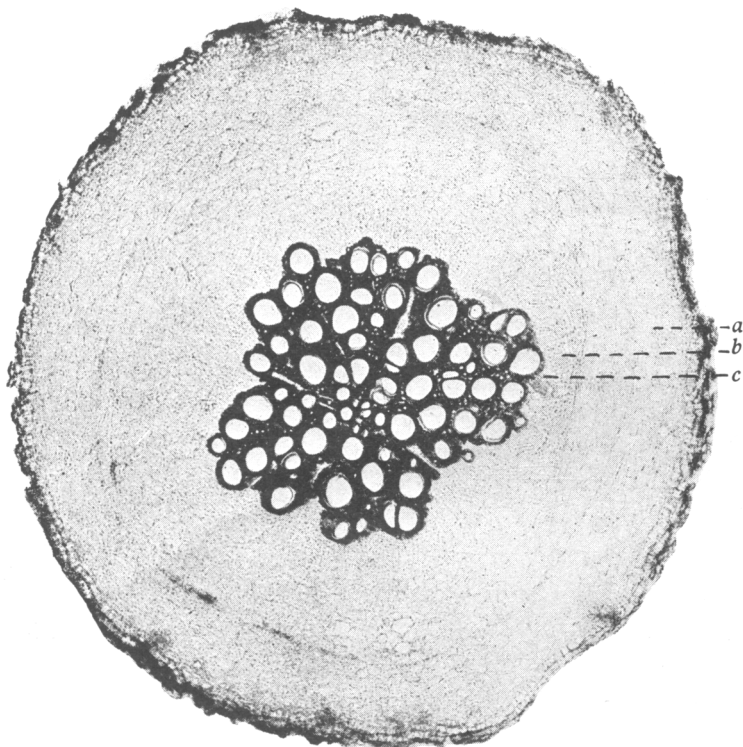


Fig. 16. Root in transverse section (X25). Depth, 7 feet 4 inches.  
*a*, Cortex; *b*, secondary phloem; *c*, secondary xylem.

The morning-glory plant normally has a taproot, with abundant laterals developing close behind the zone of root-hair formation. The function of these lateral roots is presumably the absorption of water and mineral nutrients from the soil. With the initiation of secondary growth, however, the function of the taproot becomes primarily storage and conduction, and a study of the form which it assumes shows how well it is adapted to these purposes. Successively formed xylem tubes have increased diameters as the growing season advances. These large tubes are surrounded by small, thick-walled, living, woody parenchyma cells, which strengthen and support the tissues and function in the storage of starch (fig. 16).

The tubes of the rhizome and roots vary in size between fairly constant limits. The average diameter of all the tubes in several one-year-old rhizomes was 0.055 mm. In rhizomes two years old or more, tubes averaged 0.064 mm. in diameter. A large transition-region cross section averaged 0.073 mm. in diameter in xylem tubes, while a measurement of all the tubes in thirteen cross sections of a root, taken at 6-inch intervals from a depth of 1 foot to a depth of  $7\frac{1}{3}$  feet, gave an average diameter of 0.097 mm. An average diameter of about this magnitude is found in all roots two years old or more.

The cambium of the taproot produces a large amount of secondary phloem, the function of which is primarily storage (fig. 16).

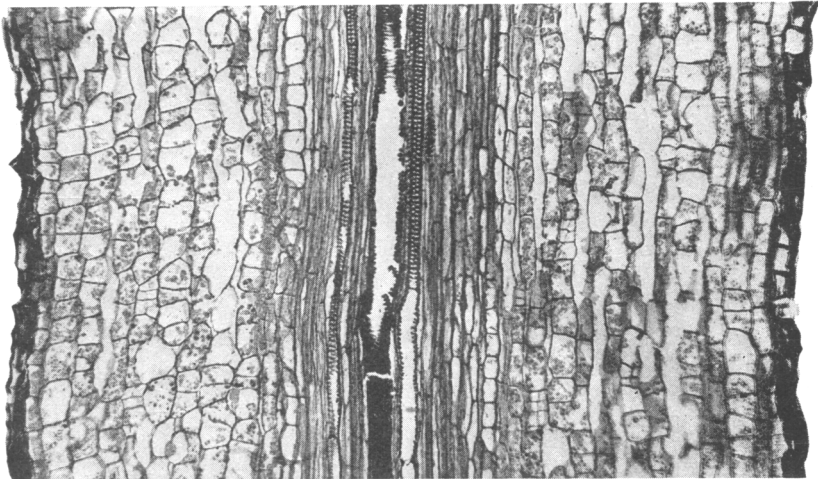


Fig. 17. Young root structure, in longitudinal section. The xylem vessels are heavily pitted, and the cortical cells filled with starch granules (X65).

The pericycle of the secondary root is not prominent. The endodermis, being held tightly together by the casparian strips, is gradually stretched until it collapses (fig. 12 and fig. 14 *C*, *D*, and *E*). Even after this, it may persist for a long time, being drawn to a thin, double-walled membrane devoid of protoplasm. Finally, it is ruptured, but fragments of the walls, with pieces of the casparian strips, were found in the oldest roots examined (fig. 14 *E*).

The cortex makes provision for increase in diameter by continued meristematic activity, and is added to by a phellogen layer, which is initiated in the hypodermis soon after secondary growth starts. The phelloderm and cortex together form a large part of the storage tissues of the mature root, the cells being completely filled with starch

during the greater part of the year (fig. 17). The phellogen forms a cork layer (phellem) on the outside, which, as it disintegrates on the surface, is continually renewed from within (fig. 18).

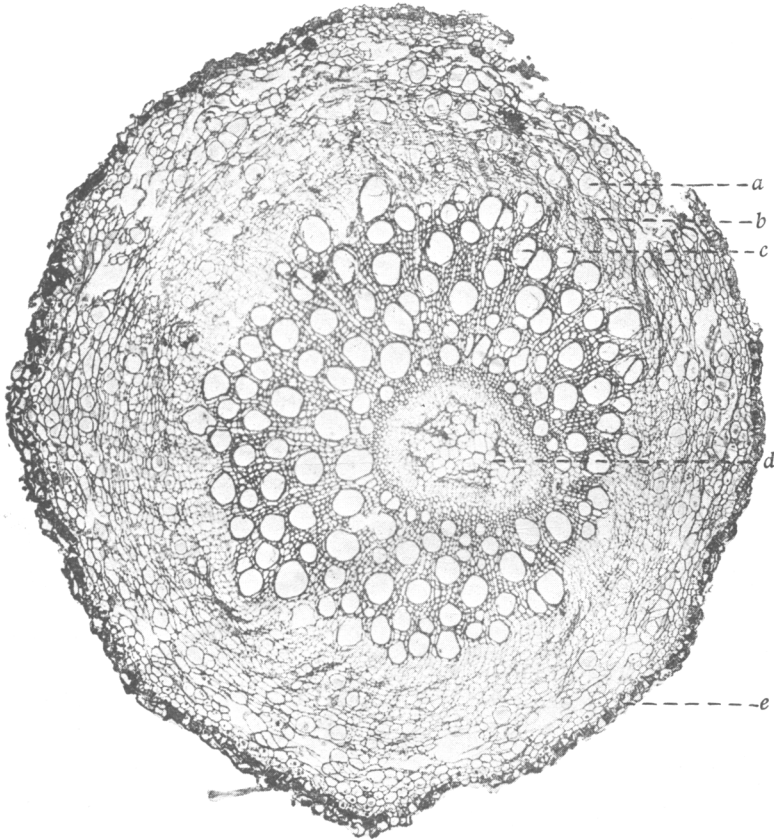


Fig. 18. Transverse section of rhizome (X40). This rhizome is several years old. The pith is being crushed by external pressure, the xylem is very similar to that of a root, and the cortex contains an unusually large number of latex vessels. *a*, Latex vessel; *b*, secondary phloem; *c*, secondary xylem; *d*, pith; *e*, phellem.

Latex vessels are more prominent in the secondary than in the primary phloem. In old roots and rhizomes, they occur in considerable numbers throughout this tissue (figs. 18 and 19).



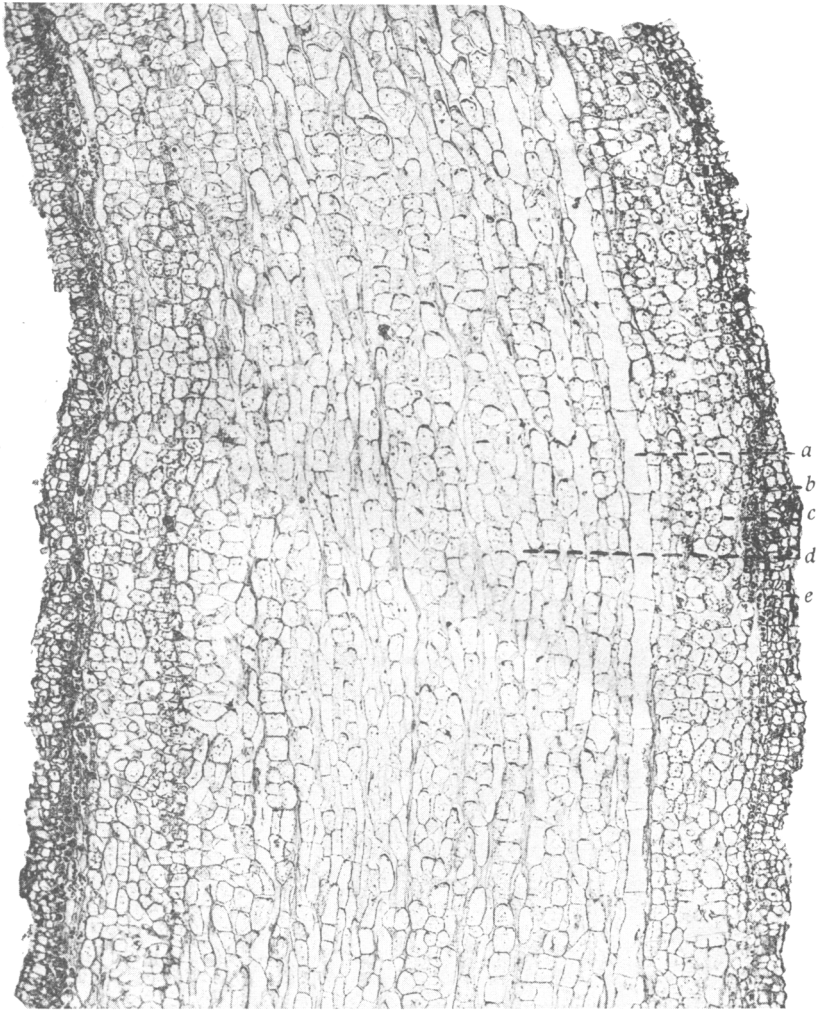


Fig. 19. Storage tissues of the root (X40). The cortex and secondary phloem are composed of a large number of living parenchyma cells and a few conducting elements. *a*, Latex vessel; *b*, phelloderm; *c*, cortex; *d*, secondary phloem; *e*, phellem.

## ANATOMICAL VARIATIONS IN THE STRUCTURE OF THE STEM AND ROOT

*The Rhizome.*—Whenever a shoot bud is produced below the surface of the ground, the stem which develops from it is a structure differing from both the ordinary stem and the true root. This is the rhizome. In it the primary vascular bundles are laid down practically

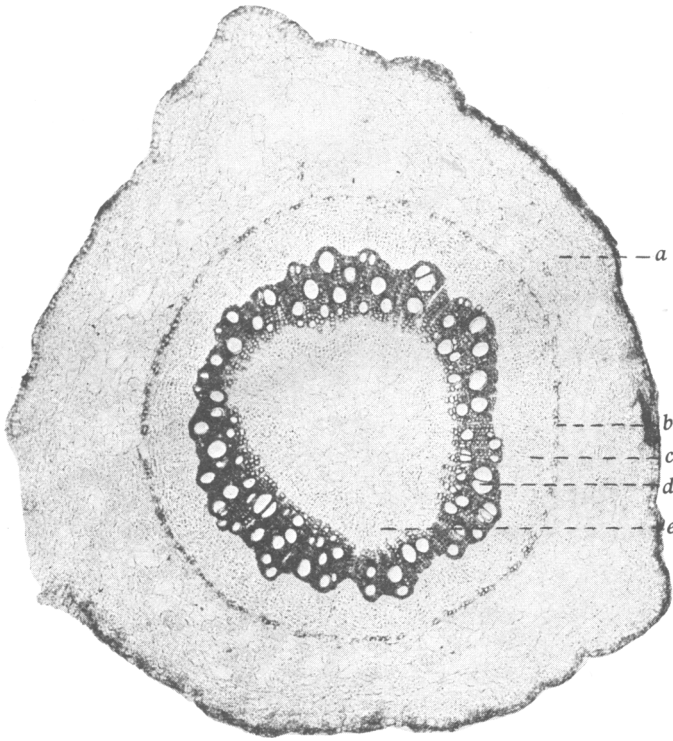


Fig. 20. One-year-old rhizome (X25). Depth, 4 inches. Note reduction of pericyclic fibers. *a*, Cortex; *b*, pericyclic fibers; *c*, secondary phloem; *d*, secondary xylem; *e*, internal phloem.

as they are in the stem (fig. 13*D*). With the initiation of secondary growth, instead of the two or three layers of vessels characteristic of the median portion of the stem xylem being formed, a mixture of very large vessels and woody parenchyma cells, identical with those of the root, is produced (figs. 20 and 21). The cambium forms an undulating band around the large tubes, and growth may be restricted to

those sides of the rhizome which have given rise to elaborate shoot growth above ground. Secondary phloem is produced in greater abundance than in the stem. Pericyclic fibers terminate a short distance below the ground level, and may be found in all stages of reduction as the rhizome is examined at increasing depths. Casparian strips in the endodermis are found in young rhizomes (fig. 13 *D*) but are not discernible in the stems above ground. The cortex is also thicker in the rhizome, resembling more closely that of the root. Chlorenchyma is wanting, and the simple epidermis is soon replaced by a periderm

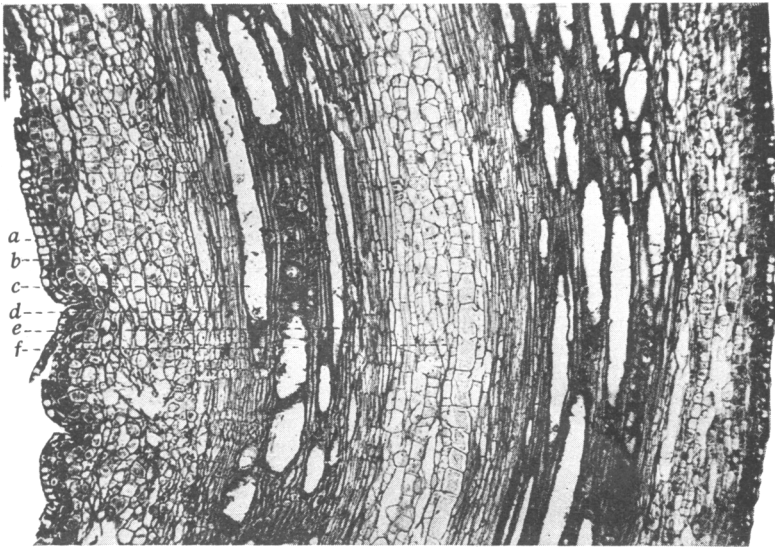


Fig. 21. Longitudinal section of a rhizome (X35). Note the relative size of the xylem vessels as compared with those of the stem. These vessels are composed of short cells with the end walls almost completely dissolved away. *a*, Pheloderm; *b*, cortex; *c*, xylem vessel; *d*, external phloem; *e*, internal phloem; *f*, pith.

similar to that of the root. Internal phloem and pith in the rhizome perform the same function as the secondary phloem and cortex; namely, storage.

The rhizome, being below ground, is protected, and persists along with the root to which it is attached. Starting from a small bud, it may develop into a structure as large as the root itself or even larger, in which case the juncture of the root and rhizome may be difficult to find. Certain characteristics, however, may enable the observer to identify it. The rhizome, except when very old, has leaf scales on the surface, a pith through the center, and leaf gaps penetrating the xylem. These are lacking in the root.

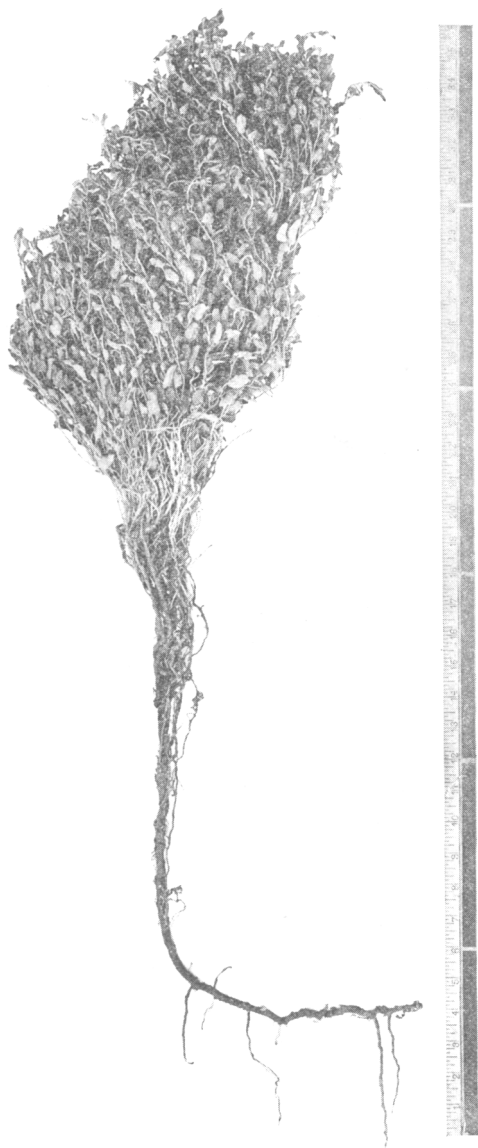


Fig. 22. Rhizome and stem development of an old root from a field that was clean cultivated for three years.

Rhizomes may vary in length from a few inches to several feet. Roots severed at various depths below the surface of the ground by gophers, or partially killed by spraying, often give rise to rhizomes several feet in length. Rhizomes may give rise to lateral roots, and, if detached from the main root, may exist independently and develop

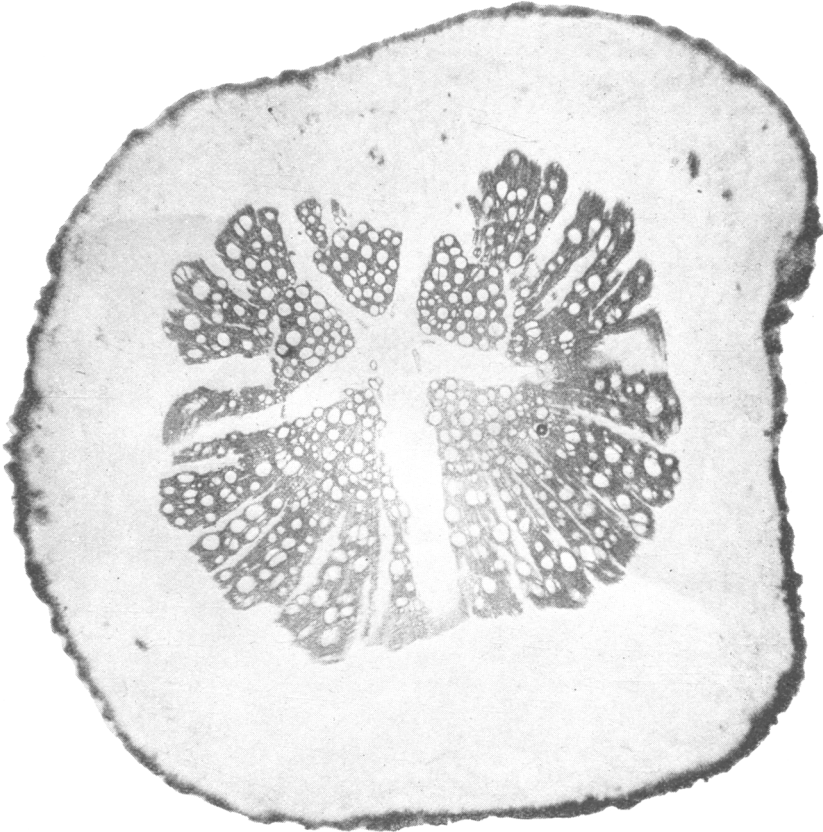


Fig. 23. Cross section of transition region showing the broad medullary rays. The groups of xylem tissues are almost completely surrounded with secondary phloem in this region (X13).

into separate plants. Whenever the taproot has become broken or cut, as in deep cultivation or plowing, the structures which connect it to the growing tops are invariably rhizomes. In many instances, old roots that have been cut off successively for several years may produce a thousand or more slender rhizomes from the severed end and give rise to a peculiar and striking bunchy form of leafy growth above ground (fig. 22).



*The Transition Region of Root and Rhizome.*—A protostele is found in the root, while a siphonostele occurs in the stem and rhizome. In the normal plant, the transition region (fig. 23) occurs just below the surface of the ground, and is characterized by prominent medullary rays, the xylem being dissected into four or five divisions. The internal phloem of the stem divides and passes out on each side of the

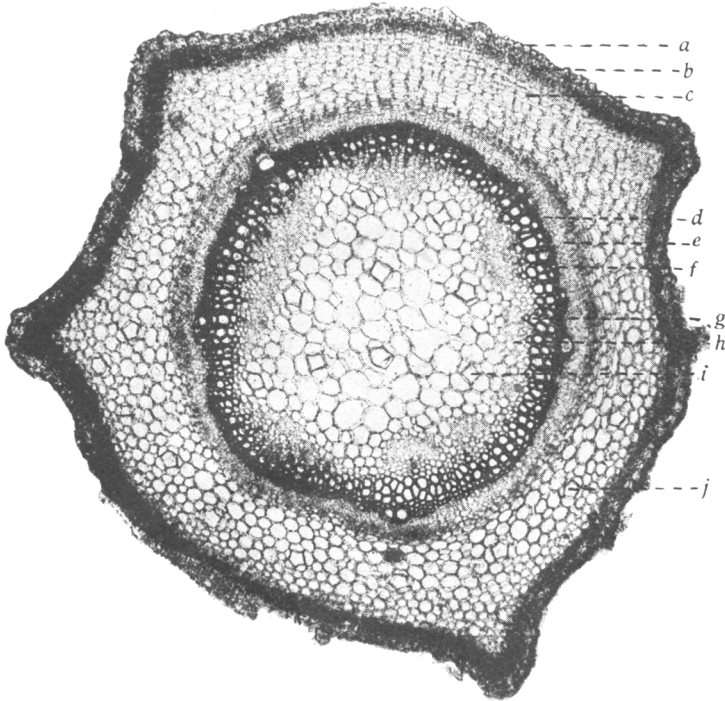


Fig. 24. Transverse section of stem (X50). Normal xylem development characterizes this stem. Latex vessels may be seen in pith and cortex. *a*, Epidermis; *b*, chlorenchyma; *c*, cortex; *d*, pericycle; *e*, external phloem; *f*, secondary xylem; *g*, primary xylem strand; *h*, internal phloem; *i*, latex vessel in pith; *j*, latex vessel in cortex.

wedge-shaped xylem segments, ultimately joining the outer phloem of the root. In the transition region, the secondary xylem is almost completely surrounded by a cambium layer which produces phloem annually. In this way, the internal phloem of the current season's stem growth is connected with the secondary phloem of the root.

In the normal plant, the transition region is short and not difficult to find. Since the great majority of plants occur in cultivated fields, where rhizomes occupy the first 6 to 10 inches of the soil, typical

transition regions occur only in occasional plants. In plants which lack the typical transition region, incursion of the protosteles usually occurs through one or two broad rays which develop from leaf gaps. In other plants where the roots divide profusely near the surface of the ground, branches from the transition region may give rise to structures of considerable length that are characterized by this dissected stele.

*Anomalous Structure.*—When a plant that has passed through its normal growth cycle and has produced in its stems the seasonal xylem tissue (fig. 24), is stimulated to new vegetative activity in any way,

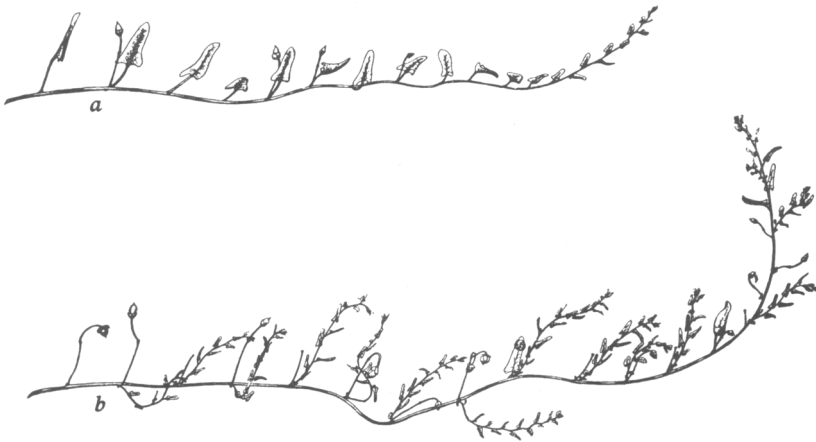


Fig. 25. Morning-glory stems.

A, Normal.

B, With shoots produced from buds in leaf-axils. The original leaves on this stem were killed by arsenic applied to an adjoining branch.

the axillary buds of the stem give rise to new shoots. The only xylem elements which occur in these buds are protoxylem tubes; these are apparently inadequate to supply water to any large transpiring surface. The xylem of the new shoot is like that of the stem from which it arises, but where it joins this parent stem it takes the form of two strands, which are produced by the cambium and superimposed upon the xylem ring previously formed. The structure of these strands is not like that of normal stem xylem but resembles the xylem of the rhizome and root. The two strands merge as they approach the base and, joining others, form a cylinder of new xylem surrounding that of the original stem. This new tissue extends through the rhizome and root and is connected distally with the most recently formed primary roots. Since it is formed at a time when transpiration is

rapid, it can be presumed that the large tubes, which may attain a diameter of 0.1 mm., are more efficient for rapid conduction of water than are the smaller xylem tubes of the normal stem.

This same effect may be produced in stems of actively growing plants by any agent which kills the leaves but not the stems. Figure

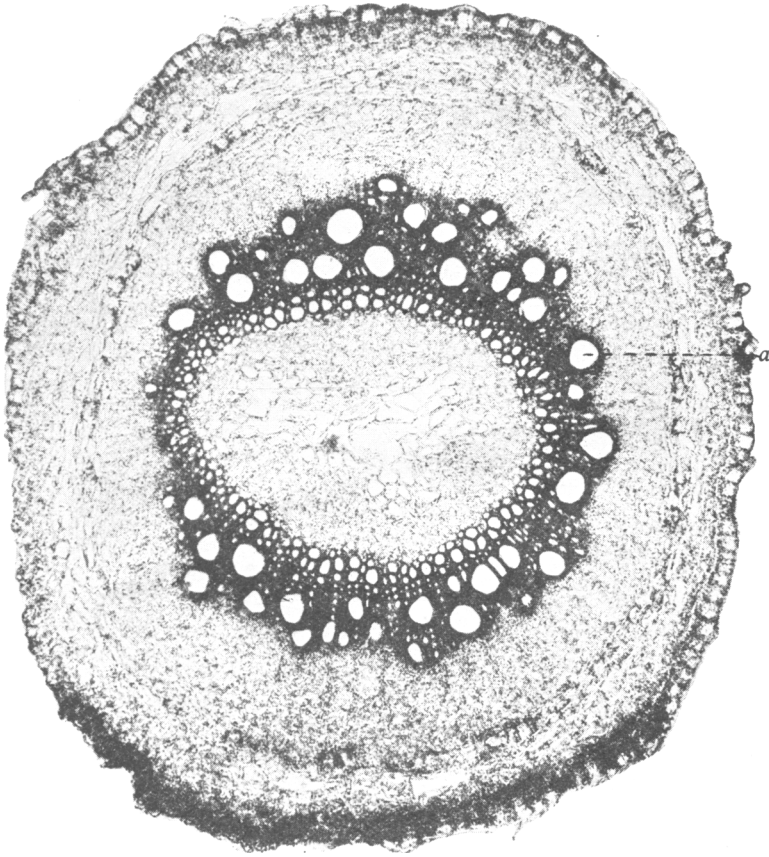


Fig. 26. Transverse section (X50) of the stem shown in figure 25B. Note effect of renewed cambial activity upon type of xylem. *a*, Xylem vessel resulting from renewed cambial activity.

25 *A* shows a normal stem and figure 25 *B* shows a stem the leaves of which were killed by submerging an adjoining stem in a dilute arsenic solution. Soon after the leaves died the axillary buds produced shoots. Figure 26 shows the effect upon the xylem of the stem; this may be compared with the xylem of the normal stem shown in figure 24.



Fig. 27. Buds on a rhizome (X30). The rhizome, like the root, can provide for rapid vegetative reproduction by the formation of buds.

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## LITERATURE CITED

<sup>1</sup> HABERLANDT, G.

1914. *Physiological plant anatomy*. 777 p. 291 figs. Macmillan & Co., Ltd., London.

<sup>2</sup> PETIT, L.

1887. *Le pétiole des dicotylédons au point de vue de l'anatomie comparée de la taxonomie*. *Mem. Soc. Sci. Bordeaux* 3:218-404. 6 pls.

<sup>3</sup> SOLEREDER, H.

1908. *Systematic anatomy of the dicots*. 2 vols. Clarendon Press, Oxford.

<sup>4</sup> EAMES A. J., and L. H. MCDANIELS.

1925. *Introduction to plant anatomy*. 364 p. 146 figs. McGraw-Hill Book Co., New York.



The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

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