THE STRUCTURE AND DEVELOPMENT OF THE STORAGE ROOT OF *HUMULUS LUPULUS* L.

by

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INTRODUCTION

The common hop, *Humulus Lupulus* L., a member of the Urticaceae, is used today chiefly in the production of beer, flavoring malt tonics and extracts and in the manufacture of near beers. The custom of using hops in beer is probably of Russian or German origin and dates back to at least the 14th century (10,p.4).

From the beginning of the 1st century A.D., various parts of the plant have been considered to be of medicinal valus; roots, stems, sap, leaves, buds, flowers and bracts being employed in various ways to cure a variety of human ills, particularly fever. Young shoots were used as human food as early as the 1st century and are still used in parts of Europe (10,p.4).

The earliest authentic reports of commercial hop culture come from France, dated 768. In America the hop seed was included among the plant introductions of the Massachusetts Company in 1629. Early commercial hop growing centered in New York state and spread gradually to northern Pennsylvania and Wisconsin. In due time hops moved to the Pacific Coast states of Oregon, Washington and California where now practically the entire commercial acreage in the United States is located (10,p.4).

For the year 1949, Oregon produced approximately 14,670,000 pounds of hops, Washington 19,380,000 pounds, California 15,290,000 pounds, Idaho 1,390,000 pounds and New York 1,650,000 pounds of hops. The United States total was 51,000,000 pounds which was approximately twice the production of any other country.

The hop is a perennial, dioecious, herbacious plant. The staminate and pistillate inflorescences are borne on separate plants, which are similar otherwise. The hop plant produces, annually, rough striated stems which twist clockwise (15,p.1217) and reach a length of 15 to 20 feet. The roughness of the stem and leaves is due to lines of strong, hooked hairs, which cause the plant to cling to its support. The leaves are petiolate, opposite, 3-5 lobed, and coarsely serrate. The upper leaves are sometimes scarcely divided, or quite entire.

The diploid number of chromosomes in H. lupulus is 20 and sex chromosomes are present. The pistillate or "female" plants have 18 autosomes plus 2 X chromosomes, while the staminate or male plants have 18 autosomes plus an X and a Y chromosome (7,p.179).

In America a few male plants are grown at various points throughout the field but in Europe these plants are excluded. In good hops the seeds are scarce, small, shrunken and sterile. Many believe that the formation of seed should be prevented, as the seeds are useless to the

brewer.

The special flavor of hop beer is due to the presence of a yellow, resin-like material called lupulin which is secreted as droplets at the base of the bracts.

The hop does not breed true from seed, so the commercial crop is grown from "root" cuttings. The cuttings are actually sections of rhizomes or underground stems. The numerous runners sent out by the hop plant just below the surface of the ground are usually removed when the plants are pruned in the spring. Some of these rhizomes, preferably ones about ½ inch in diameter, are cut into pieces approximately 6 to 8 inches long, each piece bearing at least 2 pairs of buds (11,p.5). These are then either planted directly in the field to produce new hop hills, or planted in a hot-bed and transplanted later to the field.

Two types of root systems are present in the hop plant. Long, profusely-branched fibrous roots grow just below the cultivation level. From the main horizontal roots and also from directly below the crown, medium sized roots descend vertically. These roots are irregularly swollen, fleshy and branch rarely (2,p.150).

Thus fleshy storage roots could develop from the radicle, if plants are raised from seed, or they could arise as adventitious roots from cuttings, or as branch roots on established plants.

MATERIALS AND METHODS

This study has been confined to the early development of the primary root and hypocotyl, and the development of secondary tissues in the fleshy, storage structure of field-grown hops. The latter structure probably developed as an adventitious root arising from a cutting. Hop seedlings of different ages were obtained from greenhouse germination experiments being conducted at Oregon State College. Large storage roots were obtained from a hop yard located east of Salem.

Large seedling storage roots were put in a formo-acetic-alcohol killing and fixing solution (12,p.41). Small seedlings and root tips were killed and fixed in Navashin's solution (12,p.44). A system of numbering small seedling sections before putting them into killing and fixing solutions was necessary to obtain serial slides. This was accomplished by cutting the seedlings at an angle of 90 degrees on one end of the section and 45 degrees on the other. Records were kept concerning the correct angle at the top of each section. The sections were put into separate vials to assure accuracy of serial sections.

A modified tertiary butyl alcohol schedule (12,p.130) was used for the seedlings, root tips and storage roots. After Navashin's solution was washed out of the material, generally done by putting cheesecloth covered vials in

running water, it was partially dehydrated by passing it through 15, 30, and 50 per cent alcohol, allowing 2 hours for each step. Material in formo-acetic-alcohol was washed directly in 50 per cent alcohol. All material was changed from 50 per cent alcohol to a mixture of 1 part absolute alcohol and 1 part tertiary butyl alcohol. After 2 hours, the material was changed to pure tertiary butyl alcohol, and, again after 2 hours to a mixture consisting of 3 parts tertiary butyl alcohol and 1 part xylol. After 2 hours in this solution, paraffin chips were added and the uncorked vials were placed on top of a paraffin oven. After a minimum of 6 hours and a maximum of 12 hours the material was placed inside of the oven which was set at 55 degrees centigrade. Paraffin was changed twice before the material was embedded.

A short dioxan schedule (12,p.134) and paraffins of different melting points were also tried in an attempt to improve cutting qualities of the material. In general the materials, especially pieces of older roots, sectioned better following the dioxan technique.

Root tip cross sections were cut at 12 microns and longitudnal sections were cut at 8 microns. Seedlings and storage roots were sectioned at 16 and 25 microns, respectively. Embedded seedlings were soaked in water 10 days, root tips 2 days and storage roots a maximum of 24 days.

Seedlings and storage roots were stained in 1 per cent

safranin water solution and counterstained with 0.5 per cent fast green in 3 parts clove oil and 1 part absolute alcohol, or with 0.25 per cent iron haematoxylin, used as a progressive stain. Root tips were stained in 1 per cent crystal violet water solution and 1 per cent orange G in 2 parts clove oil and 1 part absolute alcohol.

All photomicrographs except Fig. 24 were taken with a Leitz Makam, using an 8 mm. objective, N.A. 0.65 and a Leitz periplan 10x ocular. Figure 24 was taken with a B. and L. 16 mm. objective, N.A. 0.25. All negatives were enlarged when printed.

SEEDLING DEVELOPMENT

The fruit of the hop is an achene (14,p.347). The calyx is entire and the perianth closely invests the ovary which bears two long stigmas (1,p.1614). The seed possesses a spirally curved embryo and a very small amount of endosperm (13,p.337).

When the hop seed germinates the primary root emerges from the fruit coat at the stylar end, splitting the coat into halves which remain united at the base. The coat covers the cotyledons until they are pushed above the ground by hypocotyledonary growth. Approximately 10 days elapse between planting of the seed and the appearance of the young seedling above ground. The young tap root grows rapidly at first, then is retarded. Lateral roots begin to form within 3 or 4 days. During the same period the hypocotyl elongates and becomes erect. Cotyledons expand rapidly after they become free from the fruit coat. They are obovate to spatulate and taper toward their bases. The cotyledons function as photosynthetic and storage organs for a period of 2-3 weeks before drying up and falling off.

The primary xylem of the radicle is typically diarch (Fig. 1) with regard to the number of protoxylem strands developed, and is exarch with regard to the direction of differentiation of the primary xylem. The primary phloem consists of a rather broad group of phloem cells along either

side of the flat strand of primary xylem.

The primary xylem and each strand of primary phloem separates into 2 strands which move apart, with parenchyma between (Fig. 2). Each strand of xylem then separates radially into 2 strands (Fig. 3). As these are followed upward, metaxylem is differentiated more and more in a lateral position until both strands are approximately parallel with the surface (Fig. 4). This is just below the cotyledonary node. Meanwhile each phloem strand swings laterally with the xylem. All vascular strands then divide and the metaxylem differentiates toward the outside collateral bundles (Fig. 5). The 2 middle bundles come together to form the midvein of the cotyledon while the other 2 bundles remain in place to become the lateral veins (Fig. 6).

POLYSOMATY

Polysomaty is the condition in which some cells in the somatic tissues of an otherwise diploid plant contain multiples of the typical chromosome number (4,p.113). This condition occurs in the cortex of hop seeding roots where a high percentage of the cortical cells are tetraploid. The normal cortical cell has the diploid number of 20 chromosomes (Fig. 7), while the polysomatic cortical cell has the tetraploid number of 40 chromosomes (Fig. 8). Tetraploid cells can also be distinguished by their relative size since they are larger than the diploid cells of the cortex and have larger nuclei (Fig. 13).

According to Ervin (4,p.113), the origin of polysomaty in Cucumis melo L. possibly lies in a chromosome duplication in metabolic nuclei. The chromosomes at this time contain euchromocenters. A euchromocenter is a darkly stained portion of a chromosome, on both sides of the point of spindle fiber attachment, which remains chromatic in the metabolic nucleus. Ervin suggests that these euchromocenters undergo a division which is not followed by spindle formation. Under these conditions some of the sister chromosomes may remain in contact at their regions of spindle fiber attachment. Since they remain closely paired in the equatorial plate, they tend to pass to the respective poles in pairs, and hence remain somewhat paired in the ensuing telophase.

A separation during the following metabolic stage or during a subsequent division would account for the observed tetraploid cells.

While Humulus does not have true chromocenters, such are found in the cucurbits, the metabolic nuclei do show "polar cap" chromocenters. According to Heitz, as reviewed by Vanderlyn (16,pp.270,275-9,297), these are small chromocenters, located near the regions of spindle fiber attachment, which partially fuse during the telophase to form chromatic masses on the opposite sides of daughter nuclei. These "polar cap chromocenters" are well developed in Humulus (Fig. 9,12). There is not enough information at hand to determine whether this explanation for polysomaty in Cucumis can be applied to Humulus. No alternative explanation can be offered at this time.

THE PRIMARY TISSUES

The apical meristem region of the root is simpler in gross structure than that of the stem but is complicated at the tip by the root cap. Although the terms dermatogen, periblem, and plerome, indicating histogens or "tissue builders", are no longer in general use in descriptions of stem ontogeny, they have been continued for convenience to indicate general zones in the studies of root development (3,p.75). Epidermis, cortex and stele are more familiar names than dermatogen, periblem, and plerome, respectively but are derivatives of these histogens.

The hop root apparently has 3 groups of initials (Fig. 12) and follows the typical dicotyledon type of root differentiation (4,p.75). The distal initials produce the root cap and also the dermatogen which ultimately differentiates the epidermis. The medial initials produce the periblem which matures to form the cortex. The inner initials produce the plerome which differentiates the stele. The outstanding characteristic of the root apex in this group is the common origin of the root cap and epidermis. Since both these protective parts of the root develop from the same initials the cap may be looked upon as a specialized development of the epidermis (3,p.77).

The dermatogen produces epidermal cells by anticlinal divisions. The periblem divides anticlinally and also

periclinally, so that the zone becomes several layers in thickness. Subsequent divisions and differentiation result in the formation of the cortical parenchyma and endodermis. The plerome initials produce the stelar elements, consisting of primary xylem, primary phloem, and pericycle. Derivative cells divide transversely less than those of the cortex causing adjacent regions, derived from the periblem and plerome, to be distinguishable on the basis of cell size and shape.

Primary xylem and primary phloem of the root arise in the central cylinder which, in the meristematic state, is often interpreted in its entirety as the procambium strand (6,p.162). The first vascular elements to mature are a few protophloem cells which appear about 0.41 mm. above the root cap tip. These are located on opposite sides of the stele and just inside the pericycle (Fig. 13). This protophloem consists of elongated cells without nuclei but are not typical sieve tubes. About 0.55 mm. above the root cap tip differentiation of the protoxylem elements occurs on opposite marginal points of the future xylem plate (Fig. 14). The protoxylem here consist of narrow, scalariform or reticulate vessels. The points in a cross section of a stele at which xylem and phloem elements first mature are sometimes called the protoxylem and protophloem poles, respectively (5,p.184). Further primary phloem and xylem differentiate centripetally (Fig. 15). For this reason,

the primary xylem of the hop root is termed exarch in contrast to the endarch xylem characteristic of the stems of seed plants. Despite an early enlargement and vacuolation of the metaxylem, these elements develop their secondary walls slower than the protoxylem and they lose their protoplast later than the protoxylem. The primary vascular strand is complete about 0.65 mm. above the root cap tip. The metaxylem consists of vessels which are variable in size but consistantly larger than the protoxylem vessels. Also the walls of the metaxylem cells are covered with numerous, narrow bordered pits. The metaphloem consists of sieve tubes, companion cells and phloem parenchyma. The metaphloem is always separated from the metaxylem by a strip of parenchyma tissue 1-4 cells in thickness.

The endodermis is always 1 cell in thickness. Each cell develops a narrow Casparian strip which encircles the cell on the radial walls. The pericycle at this early stage is 1 or at most 2 cells in thickness. The crushed cells, seen in (Fig. 15,16), are not normal, but result from faulty technique. Pericycle fibers are differentiated in the outer pericycle region and mature approximately at the time of the first appearance of the vascular cambium (Fig. 15).

THE SECONDARY TISSUES

The increase in diameter of the storage roots of hops is largely due to the formation of secondary xylem and especially secondary phloem by the vascular cambium. The cambium originates as bands or strips of meristem in the parenchymatous tissue between the strands of primary phloem and the flattened strand of primary xylem (Fig. 15). Cambium initials are differentiated in this region, which then cut off secondary xylem cells toward the inside and secondary phloem cells toward the outside. The isolated vascular cambiums on either side of the primary xylem function for some time before they become connected around the protoxylem poles (Fig. 16). From the borders of the first-formed cambium strips the layer of initials is extended laterally by differentiation of new initials in the parenchyma between the primary phloem and xylem strands until the segments of the cambium meet in the pericycle between the xylem and endodermis (Fig. 16). Meanwhile the cells in the pericycle have divided a few times so that the pericycle opposite the protoxylem poles is now 3-5 cells in thickness.

Development of the secondary phloem proceeds rapidly after the vascular cambium becomes continuous. The pericycle parenchyma cells proliferate, by cell divisions occuring in all planes, so that the pericycle persists in spite

of the great increase in diameter. It never becomes more than a few cells in thickness, however, and never constitutes a very large portion of the fleshy storage root.

A cork cambium differentiates in the outer cells of the proliferated pericycle after considerable secondary tissue has been produced by the vascular cambium (Figs. 17, 18). The cork cambium produces cork cells on the outer face and a few or no parenchyma cells on its inner face. The cortex is killed very rapidly by the production of cork, and is soon sloughed. This cork cambium persists throughout the life of the root.

A large-celled parenchyma ray is produced by the vascular cambium opposite the strands of the protoxylem (Fig. 17). Protophloem and protoxylem show a characteristic crushing at this stage of development of the root. Pericycle fibers become scattered as a result of the proliferation of the pericycle parenchyma cells and the production of secondary tissues.

At the lower part of the hypocotyl transition region parenchyma appears in the metaxylem region (Fig. 18). In so far as the development of secondary tissues is concerned, Figure 18 represents a somewhat earlier stage than Figure 17. There are a relatively few cells of either secondary xylem or secondary phloem, the primary phloem is crushed, the pericycle fibers have not yet become scattered, and the cork cambium is just beginning to differentiate in the outer

portion of the pericycle. Casparian strips or dots, may be seen on the radial wall of the endodermis.

Details of the vascular cambium and the structure of secondary xylem and secondary phloem were also studied in large storage roots from hops growing in the field.

The vascular cambium in a well-developed storage root consist of only 2 types of initials, which are known as fusiform initials and ray initials. These are best seen in a tangential section through the cambium. The fusiform initials are long and usually tapered at both ends while the ray initials are more or less isodiametric (Fig. 19). The apparent multinucleate condition seen in some cells is due to the section being thicker than the radial dimension of the cells. The tangential walls separating the various nuclei are too thin and transparent to be seen in face view. The ray initials produce only ray cells of both xylem and phloem. The fusiform initials produce all of the other cell types which are found in the secondary xylem and phloem. The vascular cambium, as observed in cross section, proves to be of an anomalous type (Fig. 20). So far as can be determined at the present time the cambium becomes multiseriate between the vascular rays. Sieve tubes and companion cells are then differentiated in the center of this region but the cells both to the inside and the outside remain meristematic. The cambium remains approximately

uniseriate through the ray initials. The outer cambium probably does not remain indefinitely as a meristematic layer. It apparently usually divides to form parenchyma cells but it may produce sieve tubes and companion cells. After a number of cell divisions the cells in this region will all differentiate into mature cells.

As the root enlarges the later-formed secondary phloem contains fewer fibers (Fig. 21). These fibers are mucilaginous in nature. In storage roots of $\frac{1}{2}$ inch in diameter or greater, the more recently formed secondary phloem contains relatively few fibers. The phloem rays are 2-5 celled wide near the vascular cambium. As the root increases in diameter the outer portion of the rays expand in the tangential plane. This is due in part to proliferation of the ray parenchyma cells and, to a greater extent, to enlargement of the ray cells in the tangential plane.

Usually the ray initials function as an approximately uniseriate cambium but in some cases the anomalous double cambium extends across the rays (Fig. 20).

Sieve cells and companion cells differentiate early (Fig. 20). Usually there are 2-5 companion cells which extend the entire length of the sieve cell (Fig. 10). Occasionally only a single companion cell is differentiated along side the sieve cell. Young sieve cells are 5-8 times as long as their diameters. Sieve plates are simple and

each is covered with a callus plug during the winter. Callus plugs are developed when prominent cytoplasmic strands have rings formed about them at the sieve plate (3,pp.107-8). Increased deposition forms cylinders that are prominent (Fig. 10). Slime plugs (4,p.104), are also formed in young sieve cells of hop roots.

As the phloem becomes older the sieve cells lose both the callus plug and the slime bodies. The cells enlarge and the sieve plates become netted in appearance (Fig. 11). The area of the openings is greater than that of the network of wall material.

A high percentage of the secondary phloem consists of phloem parenchyma (Fig. 21). Phloem parenchyma appears in longitudinal strands of cells with the top and bottom cells being tapered. Each strand results from the transverse subdivision of a phloem initial cell cut off to the outside of the vascular cambium. Most of the phloem parenchyma cells store starch but many of them are resin cells (Fig. 21). These probably contain latex, lupulin, tannins and other substances in addition to resins. No evidence was found that would indicate that latex tubes or canals are produced in the storage roots of hops.

The vessels of the first-formed secondary xylem are large, pitted with narrow, bordered pits, simply perforated and have a thick secondary wall (Fig. 22). Muscilaginous fibers, which can be identified by shrinkage of the secondary

wall, are numerous in early secondary xylem development. Xylem parenchyma is diffuse in distribution, occuring throughout the xylem. Some of the xylem parenchyma cells also become resin cells. The xylem rays are narrow at first and some of the ray cells become filled with resin (Fig. 22).

As the storage root becomes more mature the xylem rays, which consist only of parenchyma tissue, become broader and show deposits of starch (Fig. 23). The vessels are generally smaller and tend to be in radial rows or groups. Bordered pits can be distinguished in the walls of adjoining vessels. The percentage of fibers is less here than in the first-formed secondary xylem. A lower percentage of xylem fibers is of course due to a change in cambial activity resulting in a greater percentage of xylem parenchyma cells being differentiated.

In tangenial section the wide xylem rays are prominent (Fig. 24). These rays are many cells in height. The xylem fibers are long and tapered and show secondary thickening of the mucilaginous wall with a corresponding decrease in size of the lumen. Xylem parenchyma cells are abundant. In some instances a xylem parenchyma cell becomes subdivided to form numerous, small crystalogenous cells (Fig. 24) which are usually associated with fibers.

DISCUSSION

One of the most interesting features of the development of the fleshy storage root of the hop is the more or less anomalous type of cambial activity. The differentiation of sieve tubes and companion cells in the middle of the cambium region, leaving functional cambium cells both to the inside and outside, has not been described for any other species so far as is known. The activity of the outermost cambium could probably be considered to result in "tertiary" thickening in the sense that Hayward uses it for Beta (8,p.264) and Ipomoea (8,p.495). Tertiary thickening is used to indicate any increase in diameter which is not due directly to a typical vascular cambium.

There are several unsolved problems regarding the activity of this essentially double cambium. One of these is the origin of the outer cambium. While it appears that sieve tubes and companion cells are differentiated in the middle of the cambium region, instead of on its outer face, no comparable situation has been described elsewhere. Another possibility is that such groups of sieve tubes were cut off to the outside of a single vascular cambium. Later, or perhaps simultaneously, phloem parenchyma cells outside the sieve tubes might become meristematic and then differentiate the outer cambium.

Another problem is the ultimate fate of the outer

cambium. Obviously it cannot and does not function indefinitely. Also it does not produce xylem to the inside. If so, phloem tissues would be observed embedded in secondary xylem. Such is not the case. It seems very probable that the outer cambium, at any one time, functions somewhat as was described above. The cells probably divide a few times to form either additional sieve tubes or phloem parenchyma. After these few divisions all cells of the outer cambium probably differentiate, mature, and the cambium as such disappears. Then, at this particular point in the root, the problem discussed above would arise; that is, how does a new outer cambium develop? At present the answer to this is unknown.

Sections of several fleshy storage roots have been studied and in each case this double cambium appeared. These roots were collected just before growth was resumed in the spring. It is possible that this double cambium is not present during rapid growth, but that seems unlikely. Cambial activity should be followed throughout the growing season to determine whether the double cambium is present at all times and, if so, how it is maintained.

The occurrence of polysomaty is unusual but not rare. It occurs in Spinacia, Cannabis, Acer (4,p.113) and several other genera. In most instances it is suggested that the tetraploid condition arises as a result of chromosome duplication during the metabolic condition of the nuclei.

No observed cases of nuclear fusion or abnormal mitotic behavior have been observed that would account for the tetraploid conditiin in some cells. Additional evidence is lacking here to make any definite conclusions.

The vascular rays, xylem parenchyma and phloem parenchyma are the regions of storage in fleshy hop roots. Since the amount of secondary xylem is comparatively small, the bulk of storage will be in phloem rays and phloem parenchyma. In the fleshy root of carrot (5,pp.200,217) a high percentage of the storage is in the xylem parenchyma and pericycle. In the hop storage root there is a relatively small amount of xylem parenchyma and the pericycle is only a few cells in thickness in the mature root.

SUMMARY

The transition in the hop seedling from the exarch protosteles of the radicle to the endarch collateral bundles of the cotyledons occurs mostly in the upper portion of the hypocotyl.

The cortex of the seedling root tip exhibits a high degree of polysomaty. Many of the cortical cells contain the tetraploid number of chromosomes. The diploid number is 20.

The apical meristem of the seedling root tip is of the typical dicotyledonous type. There are three plates of initial cells. The distal group produces the root cap and the epidermis; the median initials produce the cortex; the proximal group of initials produces the stele.

The radicle has a diarch protostele with exarch primary xylem. The first vascular tissue differentiated back of the growing point is the protophloem, which appears approximately 0.41 mm. back from the tip. Protoxylem first appears about 0.55 mm. back from the tip. The primary vascular strand is completely differentiated at about 0.65 mm. The endodermis is only 1 cell in thickness and the pericycle is 1-2 cells in thickness in the young seedling root.

The vascular cambium originates as isolated strips in the parenchyma tissue between each of the two strands of primary phloem and the flattened strand of primary xylem.

Later the cambium becomes continuous by differentiation of cells in the pericycle opposite the protoxylem poles.

The pericycle proliferates early and a cork cambium originates in the outer cells of this proliferated pericycle. The pericycle persists in the mature root, by continual cell division, but never becomes more than a few cells in thickness. Hence it is not an important storage region in the fleshy root. The cork cambium produces cork to the outside and few or no parenchyma cells to the inside. This cork cambium also persists throughout the life of the root.

In well-developed roots the vascular cambium is usually single across the rays and double in the regions between the rays. In between the two layers of cambium occur sieve tubes and companion cells. The origin and maintenance of this anomalous cambium has not been determined.

The vascular cambium consists of ray initials, which produce only vascular rays, and fusiform initials, which produce all of the other cell types of the secondary xylem and secondary phloem.

The secondary phloem consists of sieve tubes accompanied by usually 2-5 companion cells for each sieve tube element; phloem parenchyma cells; phloem fibers which are muscilaginous; and rays which broaden toward the outer portion of the secondary phloem. The secondary xylem consists of vessels with numerous, narrow bordered pits and

porous perforations; xylem fibers, which are muscilaginous; xylem parenchyma cells, some of which become subdivided to form small, crystalogenous cells; and rays which gradually become wider as the later formed secondary xylem is produced.

Any of the xylem or phloem parenchyma cells, vascular ray cells or pericycle parenchyma cells may store resins, tannins, lupulin and probably other substances. No indications of resin or latex canals were observed.

The principle storage cells of the fleshy root are the phloem parenchyma and phloem ray cells. Secondary xylem and proliferated pericycle constitute only a relatively small portion of the well-developed fleshy storage root.

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APPENDIX

EXPLANATION OF FIGURES 1-11

Figs. 1-6. Diagrams of cross sections through the transition region of the hypocotyl. ▩ = Primary phloem; ■ = protoxylem; ▭ = metaxylem. x250.

Fig. 7. Metaphase plate in a diploid cortical cell. x2200.

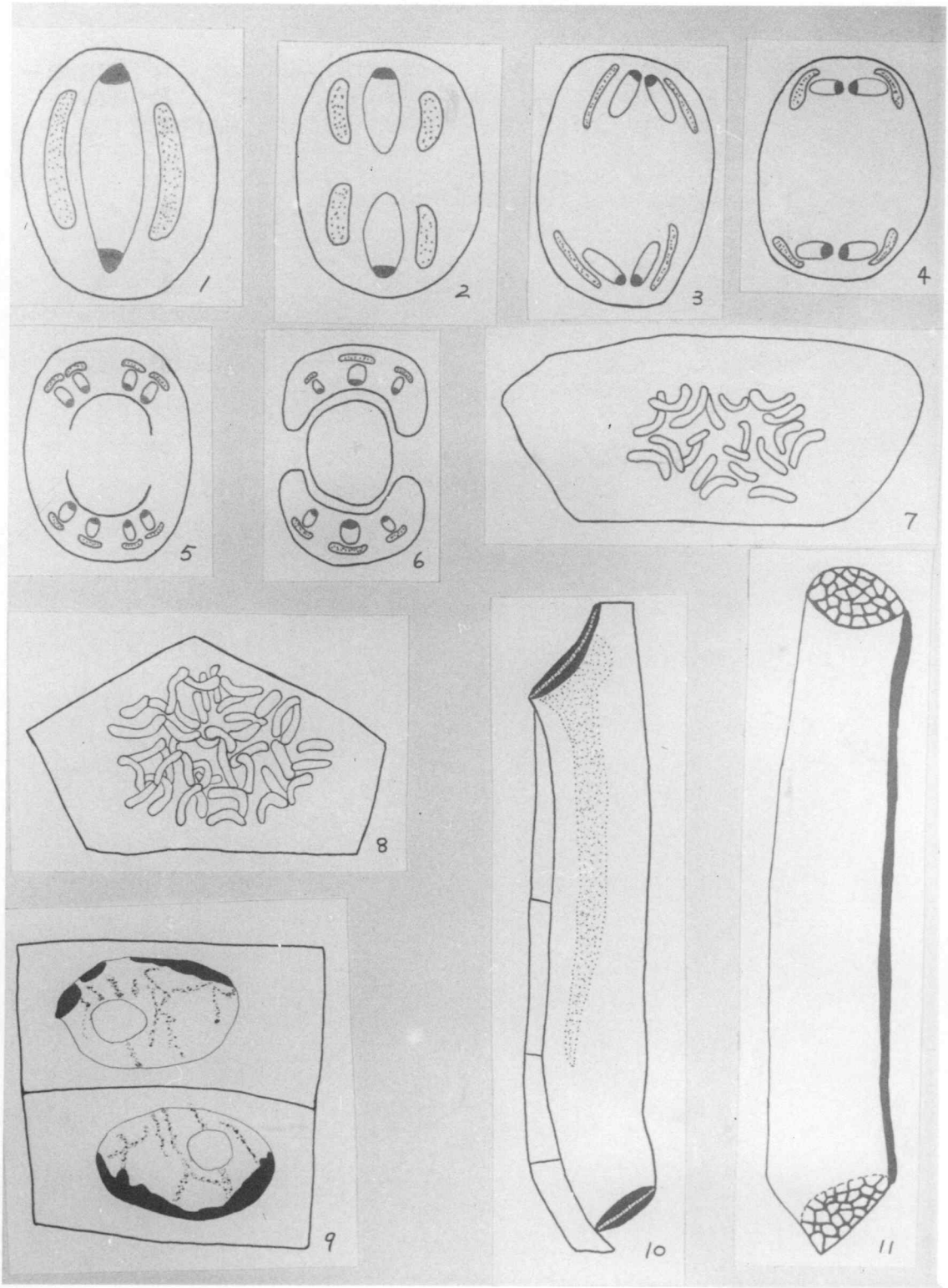
Fig. 8. Metaphase plate in a tetraploid cortical cell. x2200.

Fig. 9. Longitudinal section of daughter cells showing polar cap chromocenters. x2200.

Fig. 10. Young secondary sieve tube element and companion cells. x500.

Fig. 11. Old secondary sieve tube element and crushed companion cells. x500.

FIGURES 1-11



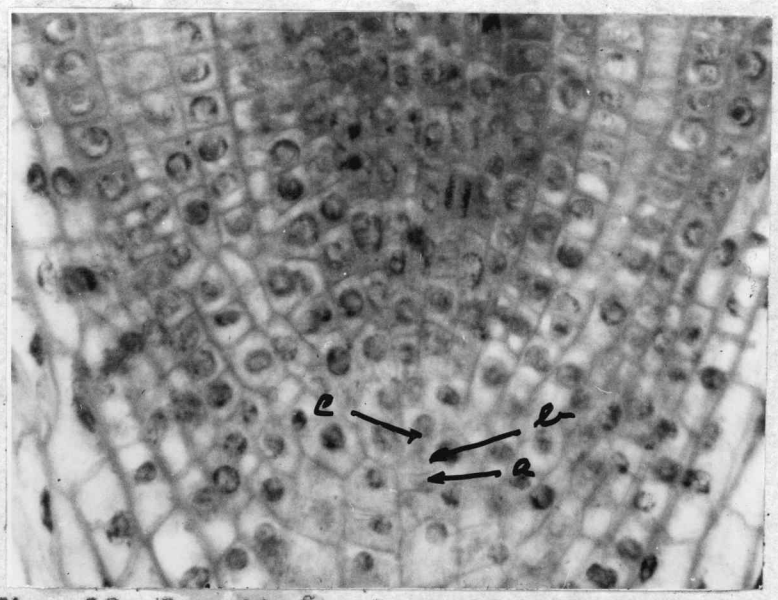


Fig. 12 Longitudinal section of apex of seedling root tip. a = initials producing root cap and epidermis; b = initials producing periblem; c = initials producing plerome. x450.

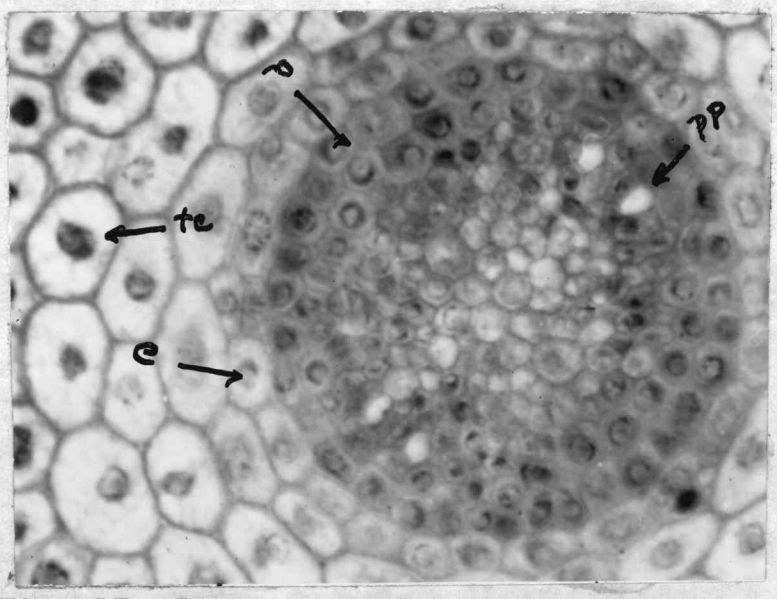


Fig. 13 Cross section of young root 0.41 mm. behind tip. pp = protophloem; e = endodermis; p = pericycle; tc = tetraploid cortical cell. x450.

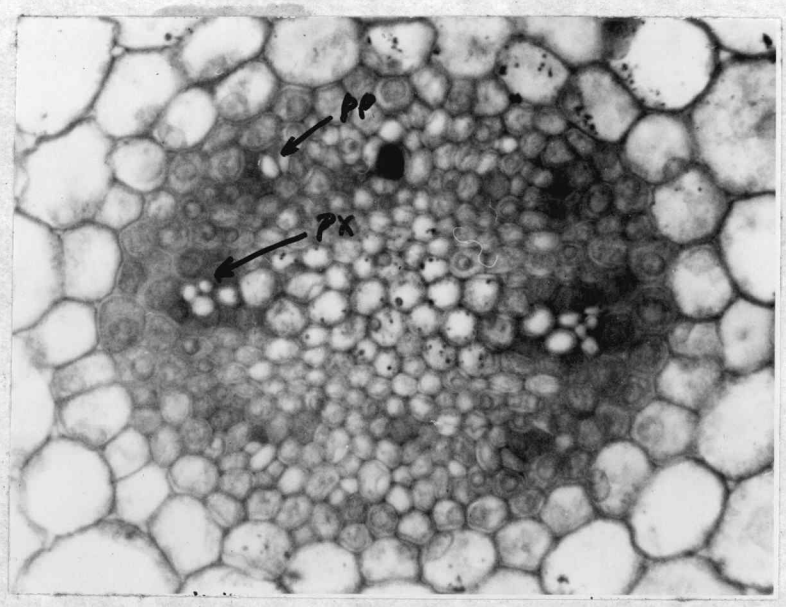


Fig. 14 Cross section of young root 0.55 mm. behind tip. pp = protophloem; px = protoxylem. x450.

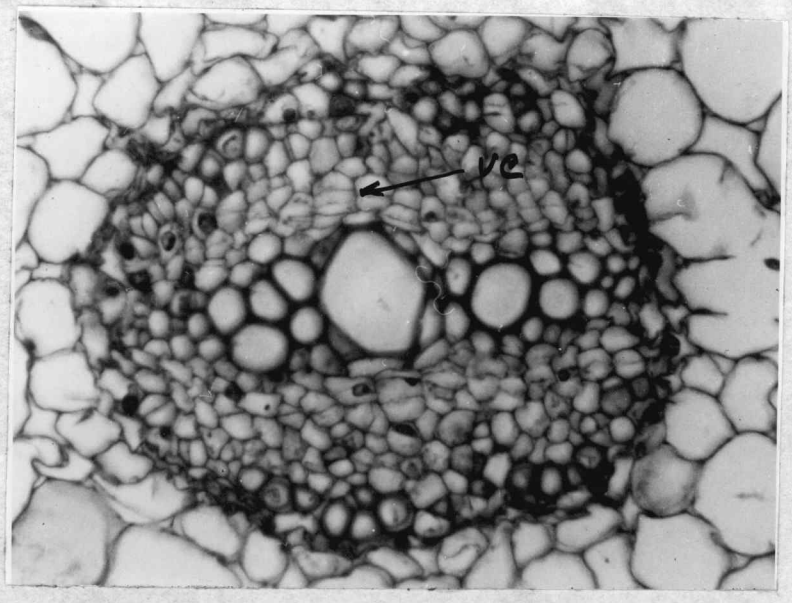


Fig. 15 Cross section of stele after maturation of primary tissues. vc = initiation of vascular cambium. x450.

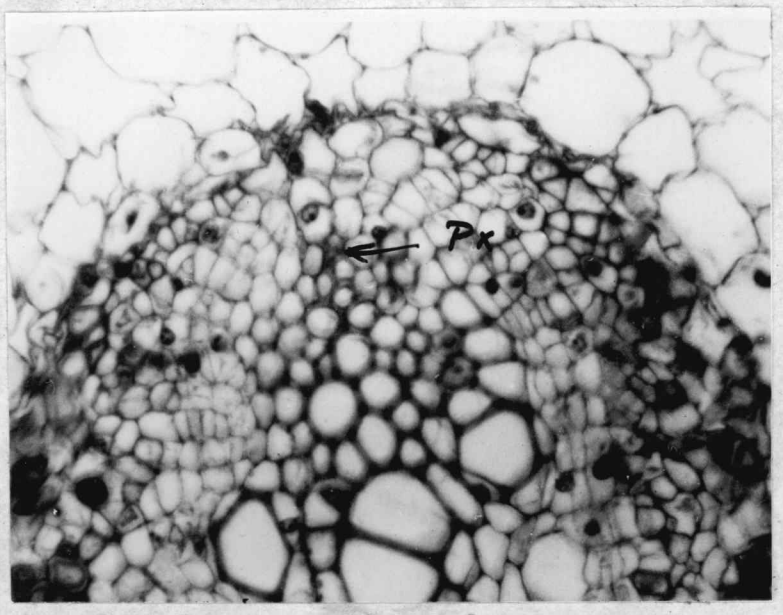


Fig. 16 Cross section of young root showing the vascular cambium developing in the pericycle opposite a protoxylem pole. px = protoxylem. x450.

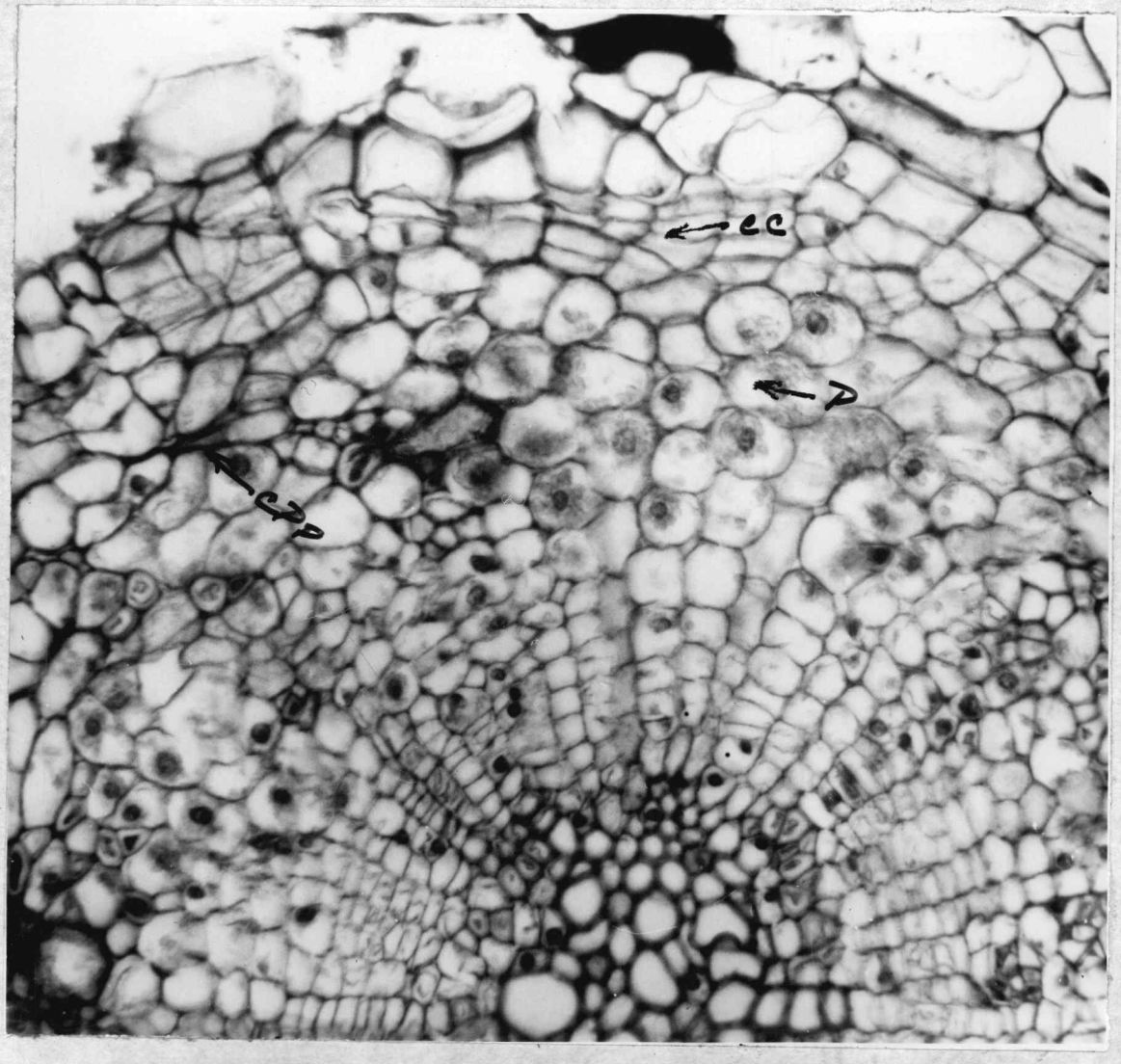


Fig. 17 Cross section of root at time of the initiation of the cork cambium. cc = cork cambium; p = pericycle; cpp = crushed primary phloem. x450.

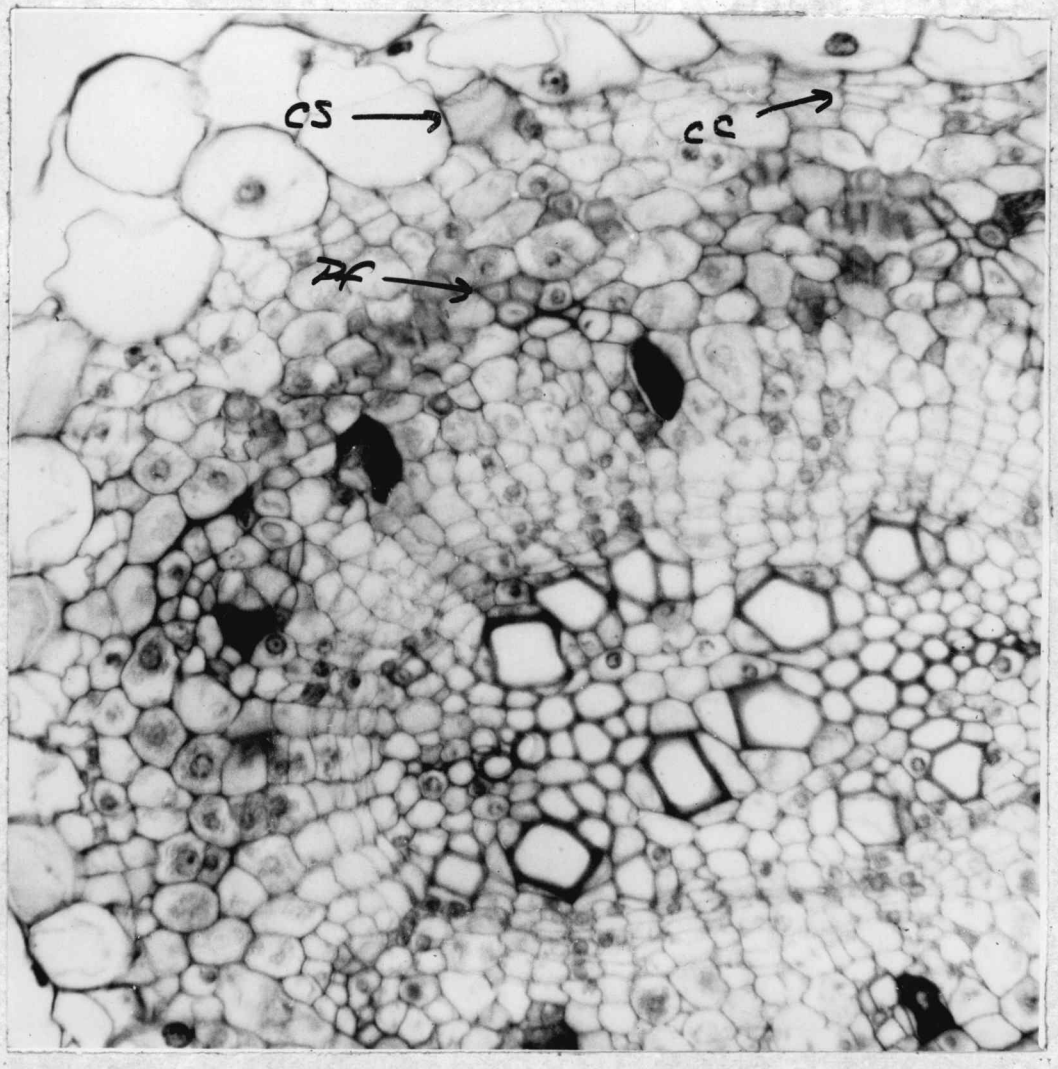


Fig. 18 Cross section through upper part of radicle. cs = casparian strip on endodermis cell; cc = cork cambium; pf = pericycle fiber. x450.

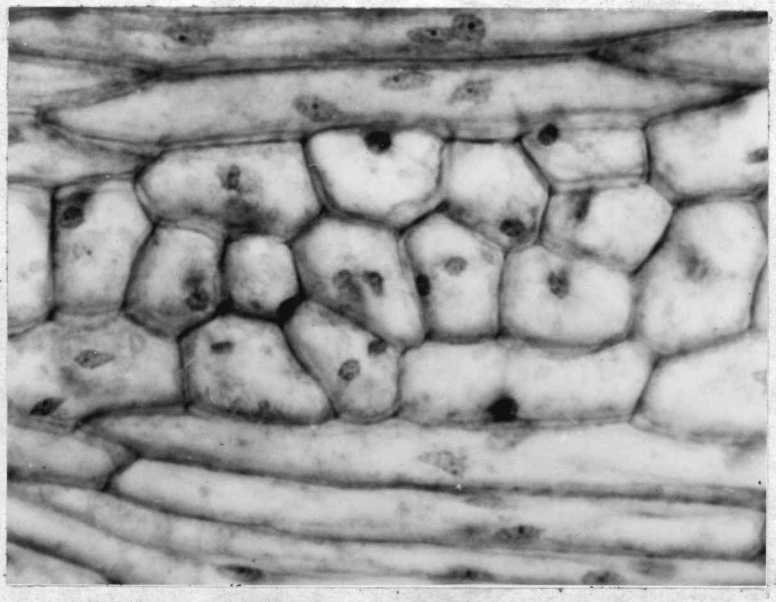


Fig. 19 Tangential section of the vascular cambium showing ray initials and fusiform initials. x450.

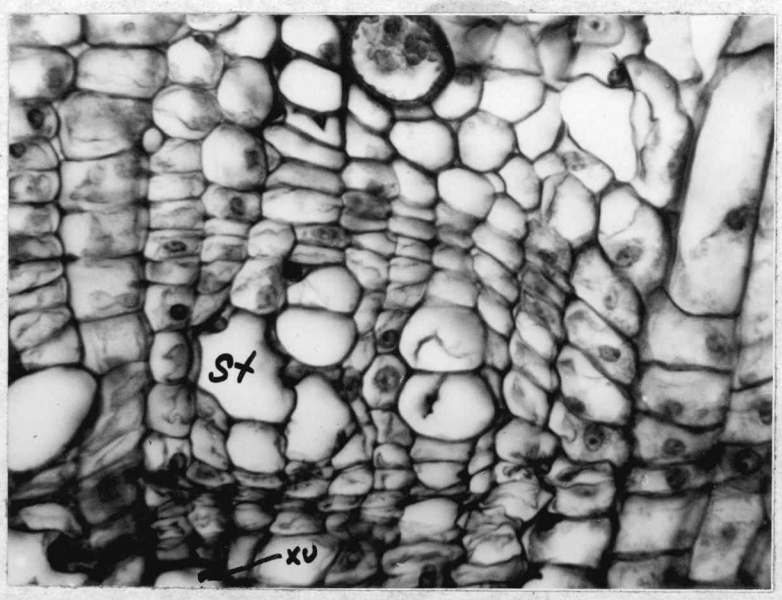


Fig. 20 Cross section showing anomalous type of cambial activity. st = sieve tube; xv = secondary xylem vessel. x450.

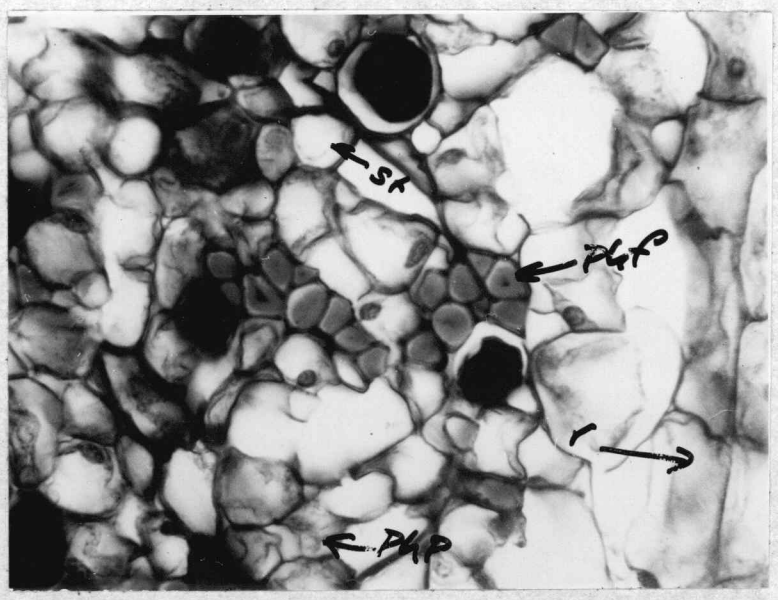


Fig. 21 Cross section of older secondary phloem. st = sieve tube; php = phloem parenchyma; phf = phloem fiber; r = ray. x450.

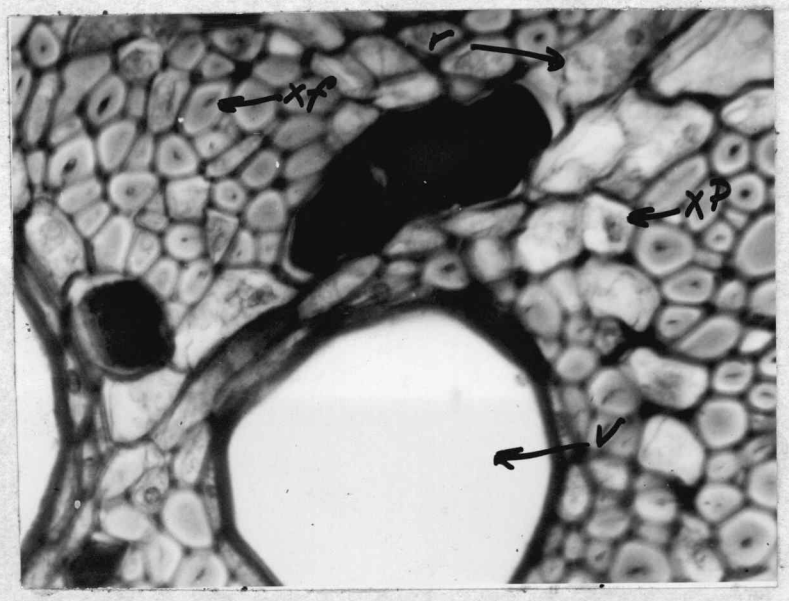


Fig. 22 Cross section of first-formed secondary xylem. xf = xylem fiber; xp = xylem parenchyma; r = ray; v = vessel. x450.

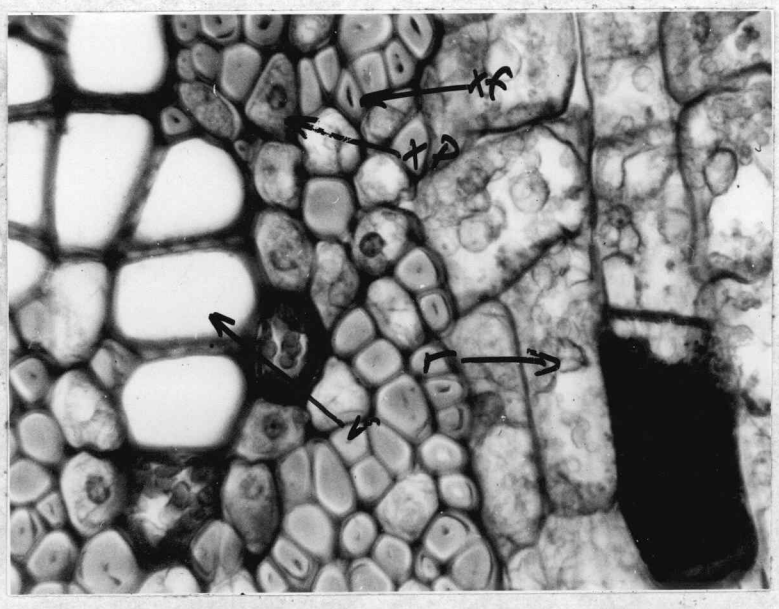


Fig. 23 Cross section of later-formed secondary xylem. xf = xylem fiber; xp = xylem parenchyma; r = ray; v = vessel. x450.

Fig. 24 Tangential section of later-formed secondary xylem exclusive of vessels. xf = xylem fibers; xp = xylem parenchyma; r = ray; crc = crystalogenous cell. x220.