SARDAR PATEL UNIVERSITY
B. Sc. (BOTANY)Sem. : VI Paper Code : US06CBOT22 (T)
Title of Paper : ANATOMY OF ANGIOSPERMS
Total Credit : 4 (Four Lectures per week)
(Total Marks 100, Internal-30 marks, External 70-marks)
Syllabus with effect from: June 2020

UNIT CONTENT : 3. Vascular Cambium and Wood :
Structure, function and seasonal activity of cambium; Secondary growth in root and stem. Axially and radially oriented elements; Types of rays and axial parenchyma; Cyclic aspects and reaction wood; Sapwood and heartwood; Ring and diffuse porouswood; Early and late wood, tyloses; Dendrochronology. Development and composition of periderm, rhytidome and lenticels.

Structure, function and seasonal activity of cambium;

1. Origin of Cambium 2. Fascicular and Inter-fascicular Cambium 3.Duration 4.Functions 5. Structure 6. Cell Division .

1. Origin of Cambium :

The primary vascular skeleton is built up by the maturing of the cells of the procambium strands to form xylem and phloem. The plants which do not possess secondary growth, all cells of the procambium strands mature and develop into vascular tissue.

In the plant which have secondary growth later on, a part of the procambium strand remains meristematic and gives rise to the cambium proper. In roots the formation of cambium differs from that in stems because of the radial arrangement of the alternating xylem and phloem strands.

Here the cambium arises as discrete(individually) strips of tissue in the procambium strands inside the groups of primary phloem. Later on, the strips of cambium by their lateral extension are joined in the pericycle opposite the rays of primary xylem. The secondary tissue formation is most rapid beneath the groups of phloem so that the cambium, as seen in the transverse section of older roots, soon forms a circle.

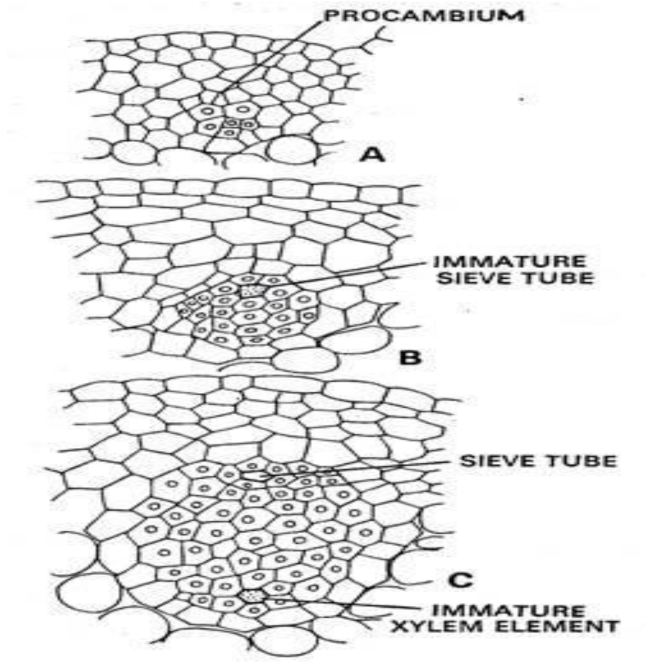

Fig. 39.1. Primary vascular differentiation, A–C, successive stages in the development of the proceambium in T.S. of *Linum* stem. The first phloem and xylem elements begin to differentiate before procambial strand completes its increase in diameter.

2. Fascicular and Inter-fascicular Cambium:

In stems the first procambium that develops from promeristem is usually found in the form of isolated strands. In some plants these first-formed strands soon become, united laterally by additional similar strands formed between them and by the lateral extention of the first-formed strands.

During further development this procambial cylinder gives rise to a cylinder of primary vascular tissue (xylem and phloem) and cambium. Later on, a cylinder of secondary vascular tissue is formed that arises in strands as does the primary cylinder. In Ranunculus and some other herbaceous plants, the procambium strands, and the primary vascular tissues, do not fuse laterally but remain as discrete strands.

More often in herbaceous stems the cambium extends laterally across the intervening spaces until a complete cylinder is formed. Where such extension occurs, the cambium arises from inter-fascicular meristematic cells derived from the apical meristem.

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The strips of cambium that arise within collateral bundles are known as fascicular cambium, and the cambial strips found in between the bundles are known as inter-fascicular cambium.

3. Duration of Cambium:

The duration of the functional life of the cambium varies greatly in different species and also in different parts of the same plant. In a perennial woody plant the cambium of the main stem lives from the time of its formation until the death of the plant.

It is only by the continued activity of the cambium in producing new xylem and phloem that such plants can maintain their existence. In leaves, inflorescenes and other deciduous parts, the functional life of the cambium is short. Here all the cambium cells mature as vascular tissue. The secondary xylem is directly found upon the secondary phloem in such bundles.

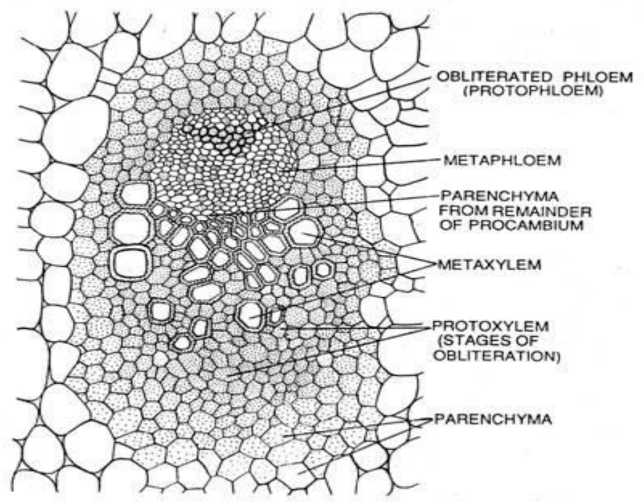

Fig. 39.2. The stem. T.S. of a vascular bundle of *Ranunculus*. This is an example of collateral bundle from a herbaceous dicotyledon lacking secondary growth. (After K. Esau.)

4. Function of Cambium : The meristem that forms secondary tissues consists of an uniseriate sheet of initials that form new cells usually on both sides. The cambium forms xylem internally and phloem externally. The tangential division of the cambial cell forms two apparently identical daughter cells.

One of the daughter cells remains meristematic, i.e., the persistent cambial cell, the other becomes a xylem mother cell or a phloem mother cell depending upon its position internal or external to the initial. The cambium cell divides continuously in a similar way; one daughter cell always remains meristematic, the cambium cell, whereas the other becomes either a xylem or a phloem mother cell.

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Probably there is no definite alternation and for brief periods only one kind of tissue is formed. Adjacent cambium cells divide at nearly the same time, and the daughter cells belong to the same tissue. This way, the tangential continuity of the cambium is maintained.

5. Structure of Cambium : There are two general conceptions of the cambium as an initiating layer:

1. That it consists of a uniseriate layer of permanent initials with derivatives which may divide a few times and soon become converted into permanent tissue;

2. That there are several rows of initating cells which form a cambium zone, a few individual rows of which persist as cell forming layers for some time. During growing periods the cells mature continuously on both sides of the cambium it becomes quite obvious that only a single layer of cells can have permanent existence as cambium.

Other layers, if present, function only temporarily and become completely transformed into permanent cells. In a strict sense, only the initials constitute the cambium, but frequently the term is used with reference to the cambial zone, because it is difficult to distinguish the initials from their recent derivatives.

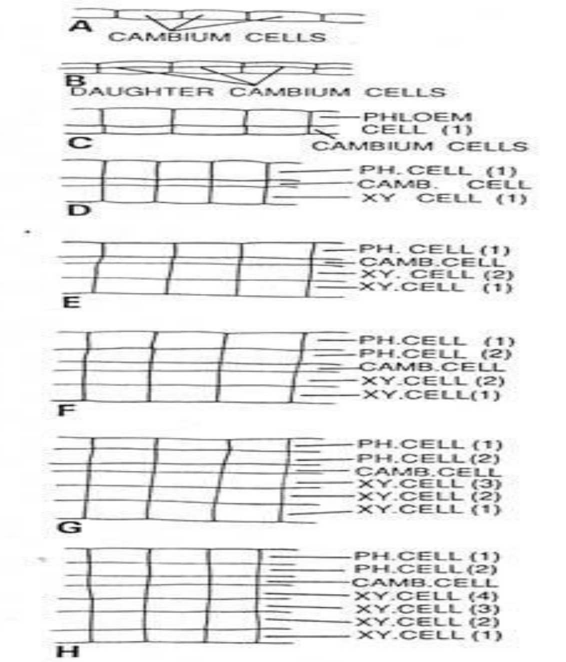

Fig. 39.3. The cambium. A—H, diagrams showing the formation of xylem and phloem by the cambium, and changes in position of phloem and cambium by this activity.

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Cellular Structure of Cambium:

There are two different types of cambium cells:

1. The ray initials, which are more or less isodiametric and give rise to vascular rays; and

2. The fusiform initials, the elongate tapering cells that divide to form all cells of the vertical system.

The cambial cells are highly vacuolated, usually with one large vacuole and thin peripheral cytoplasm. The nucleus is large and in the fusiform cells is much elongated. The walls of cambial cells have primary pit fields with plasmodesmata. The radial walls are thicker than tangential walls, and their primary pit fields are deeply depressed.

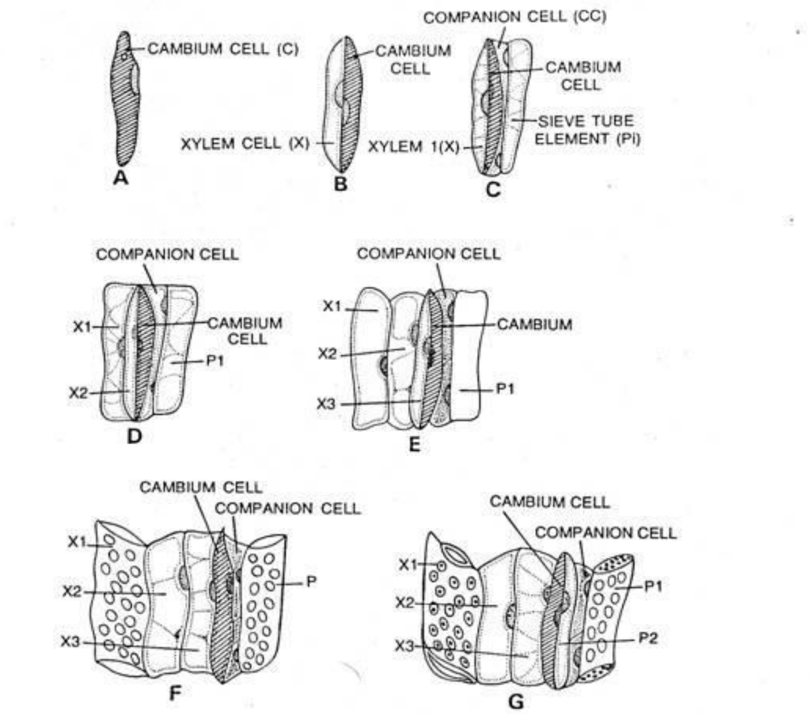

Fig. 39.4. The cambium. Differentiation of phloem and xylem from vascular cambium. A—G, diagrams as seen in radial section, showing stages in differentiation of vascular cambium cells.

6. Cell Division in Cambium :

With the result of tangential (periclinal) divisions of cambium cells the phloem and the xylem are formed. The vascular tissues are formed in two opposite directions, the xylem cells towards the interior of the axis, the phloem cells toward its periphery. The tangential divisions of the cambium initials during the formation of vascular tissues determine the arrangement of cambial derivatives in radial rows.

Since the division is tangential, the daughter cells that persist as cambium initials increase in radial diameter only. The new cambium initials formed by transverse divisions increase greatly in length; those formed by radial divisions do not increase in length.

As the xylem cylinder increases in thickness by secondary growth, the cambial cylinder also grows in circumference. The main cause of this growth is the increase in the number of cells in tangential direction, followed by a tangential expansion of these cells.

Cambium Growth about Wounds : One of the important functions of the cambium is the formation of callus or wound tissue, and the healing of the wounds. When wounds occur on plants, a large amount of soft parenchymatous tissue is formed on or below the injured surface; this tissue is known as callus. The callus develops from the cambium and by the division of parenchyma cells in the phloem and the cortex.
During the healing process of a wound the callus is formed. In this there is at first abundant proliferation of the cambium cells, with the production of massive parenchyma. The outer cells of this tissue become suberized, or periderm develops within them, with the result a bark is formed.

However, just beneath this bark the cambium remains active and forms new vascular tissue in the normal way. The new tissue formed in the normal way extends the growing layer over the wound until the two opposite sides meet. The cambium layers then unite and the wound becomes completely covered.

Cambium in Budding and Grafting : In the practices of budding and grafting, the cambium of both stock and scion gives rise to callus which unites and develops a continuous cambium layer that gives rise to normal conducting tissue. There is an actual union of the cambium of stock and scion of two plants during the practices of budding and grafting and therefore these practices are not commonly found in monocotyledons.

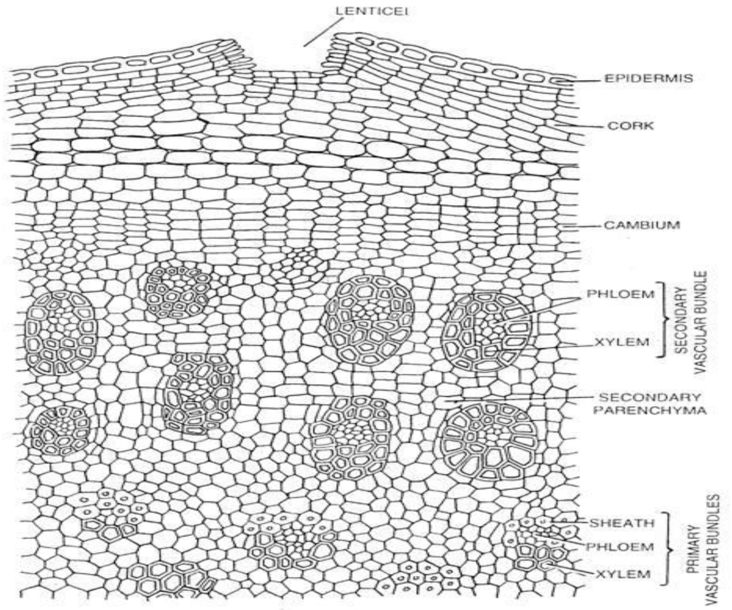

Fig. 39.5. T.S. of a portion of stem of *Dracaena* (monocot) showing secondary growth.

Cambium in Monocotyledons:

A special type of secondary growth occurs in few monocotyledonous forms, such as Dracaena, Aloe, Yucca, Veratrum and some other genera. In these plants the stem increases in diameter forming a cylinder of new bundles embedded in a tissue.

Here a cambium layer develops from the meristematic parenchyma of the pericycle or the innermost cells of the cortex. In the case of roots, the cambium of this develops in the endodermis. The initials of cambium strand in tiers to form a storied cambium as found in the normal cambium of some dicotyledons.

The activity of the primary thickening meristem resembles with secondary growth found in certain monocotyledons such as Dracaena, Yucca, etc. The apical meristem also known as shoot apex produces only small part of the primary body, i.e., a central column of parenchyma and vascular strands.

Most of the plant body is formed by the primary thickening meristem. The primary thickening meristem is found beneath the leaf-primordia, which divides periclinally producing anticlinal rows of cells. These cells differentiate into a tissue formed of ground parenchyma traversed by procambial strands.
These procambial strands later on develop into vascular bundles. The ground parenchyma cells enlarge and divide repeatedly, causing increase in thickness. This way, both apical meristem and primary thickening meristem give rise to the main bulk of the stem tissues of monocotyledons.

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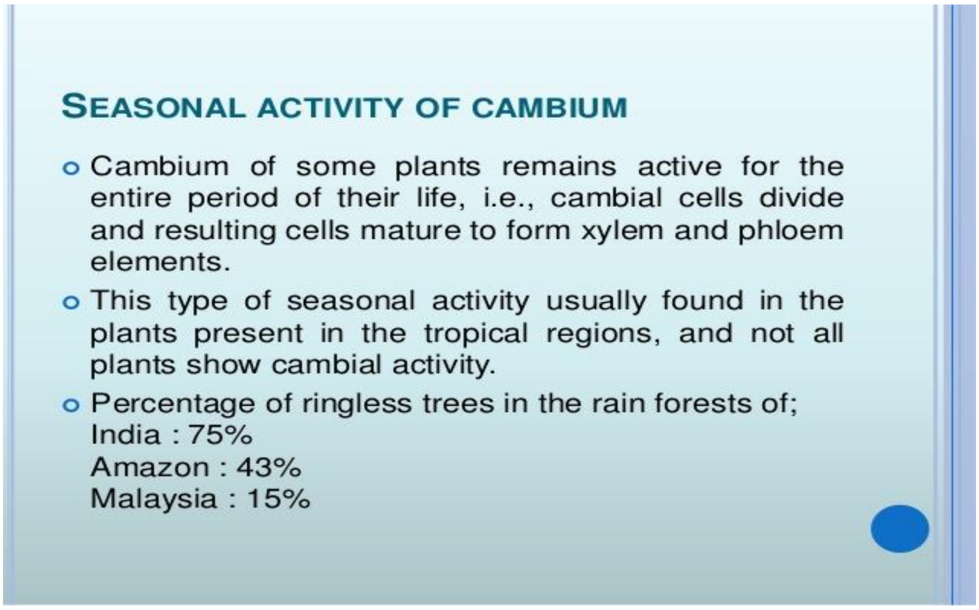
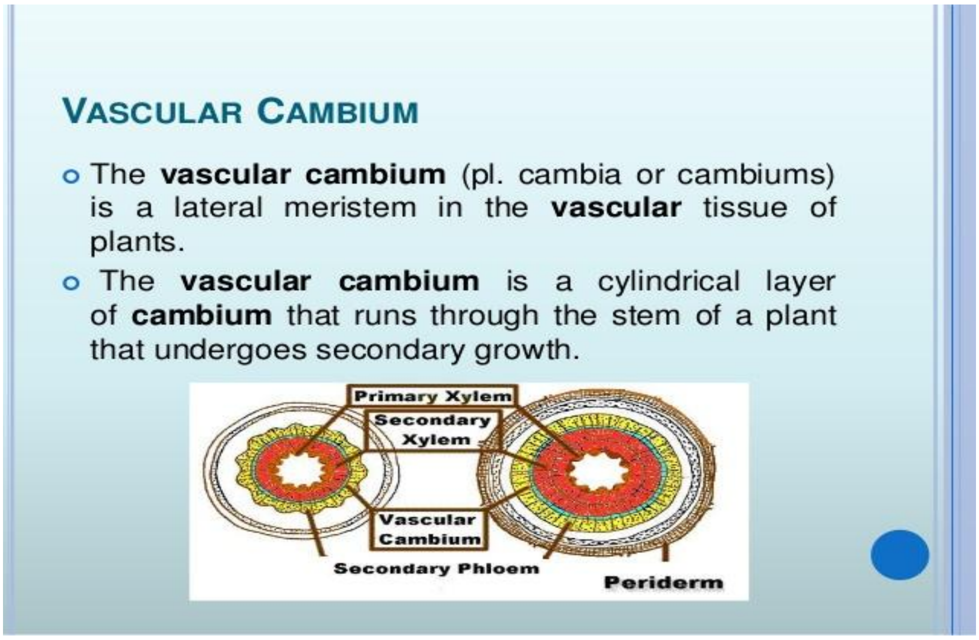
The thickening takes place in monocotyledons, such as palms, due to the activities of the apical meristem and primary thickening meristem.





- In regions with definite seasonal climate; seasonal activity of cambium ceased with onset of unfavorable conditions; In Autumn, it enters the dormant state and lasts for the end of summer; In Spring, cambium again becomes active.
- Duration of cambial activity is also affected by day-length, e.g., In ***Robinia pseudoacacia,*** cambium is dormant under short-day condition.

LOCATION OF VASCULAR CAMBIUM

In Dicots:

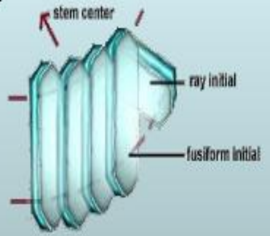
The **vascular cambium** is in dicot stems and roots, located between the xylem and the phloem in the **stem** and root of a **vascular** plant, and is the source of both the **secondary** xylem **growth** (inwards, towards the pith) and the **secondary** phloem **growth** (outwards).

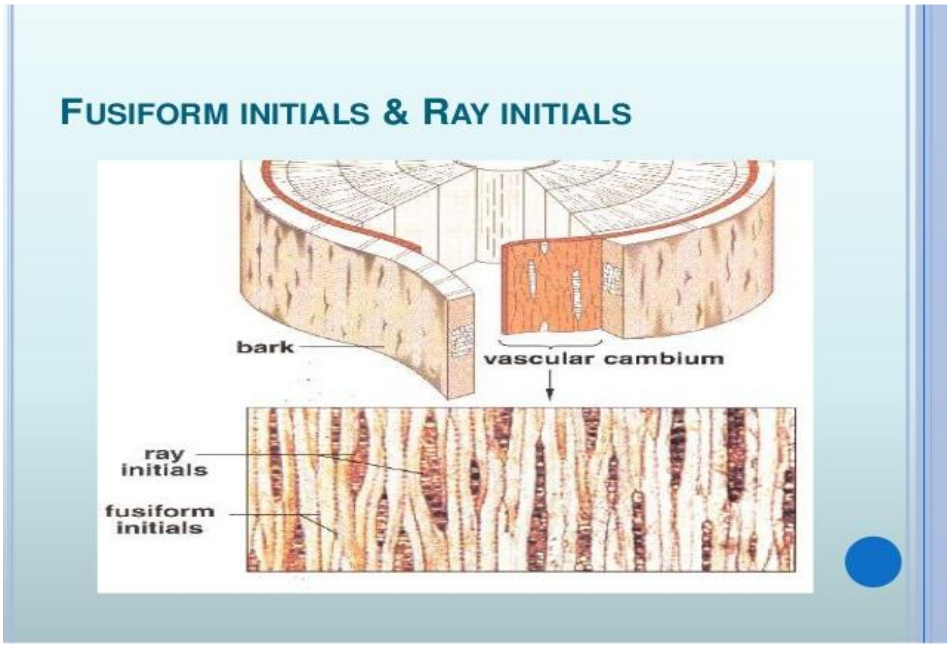
In Monocots:

Monocot stems, such as corn, palms and bamboos, **do** not **have a vascular cambium** and **do** not exhibit secondary growth by the production of concentric annual rings. They cannot increase in girth by adding lateral layers of cells as in conifers and woody dicots.

TYPES OF CELLS

Vascular cambium is a very thin layer that lies between the primary xylem inside and primary phloem on outside. They contain meristematic cells that can form the secondary xylem inside and secondary phloem outside. There are two kinds of meristematic cells called **fusiform initials** which are vertically elongated and **ray initials** which are horizontally elongated.





Secondary Growth in Dicotyledonous Roots :

1. Introduction to Secondary Growth 2. Formation of Cambium and Development of Secondary Tissues 3.Periderm.

Introduction to Secondary Growth :

The roots of gymnosperms and most dicotyledonous undergo secondary growth. Most of the dicotyledonous roots show secondary growth in thickness, similar to that of dicotyledonous stems. However, the roots of extant vascular cryptogams and most monocotyledons do not show any secondary growth; they remain entirely primary throughout their life.

The secondary tissues developed in the dicotyledonous roots are fundamentally quite similar to that of dicotyledonous stems, but the process initiates in some different manner. Certain dicotyledonous roots do not show secondary growth. The secondary vascular tissues originate as a result of the cambial activity. The phellogen gives rise to the periderm.

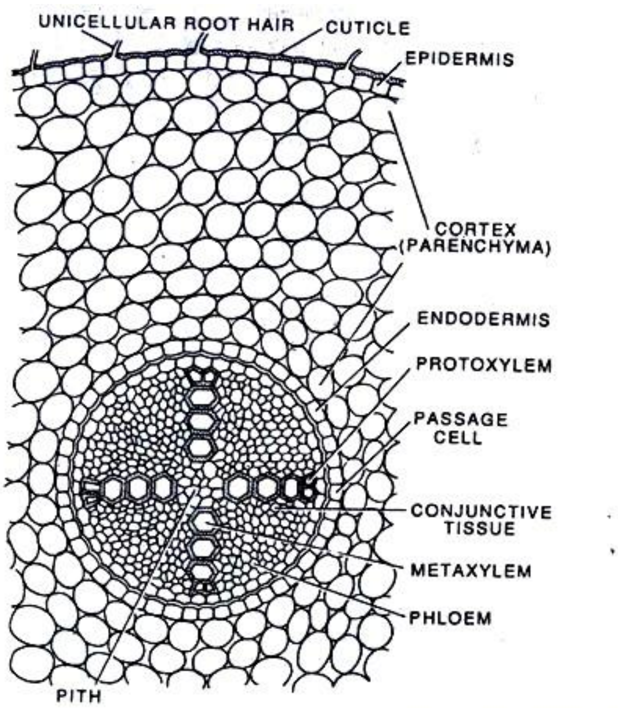


Fig. 42.43. The root. T.S. of a dicotyledonous (gram) root showing tetrarch xylem and small pith.

Formation of Cambium and Development of Secondary Tissues: The dicotyledonous roots posses a limited number of radial vascular bundles with exarch xylem. Normally the pith is very little or altogether absent. On the initiation of secondary growth, a few parenchyma cells beneath each group of phloem

become meristematic and thus as many cambial strips are formed as the number of phloem groups.
The cambial cells divide tangentially again and again and produce secondary tissues. Thereafter some of the cells of single layered pericycle become meristematic lying against the protoxylem groups, which divide and form a few layers of cells. The first formed cambium now extends towards both of its edges and reaches the inner most derivatives of the pericycle, thus giving rise to a complete ring of cambium.The cambium ring is wavy in outline, as it passes internal to phloem and external to xylem groups. The cambial cells produce morexylem elements than phloem. The first formed cambium produces secondary xylem much earlier, and the wavy cambium ring ultimately becomes circular.

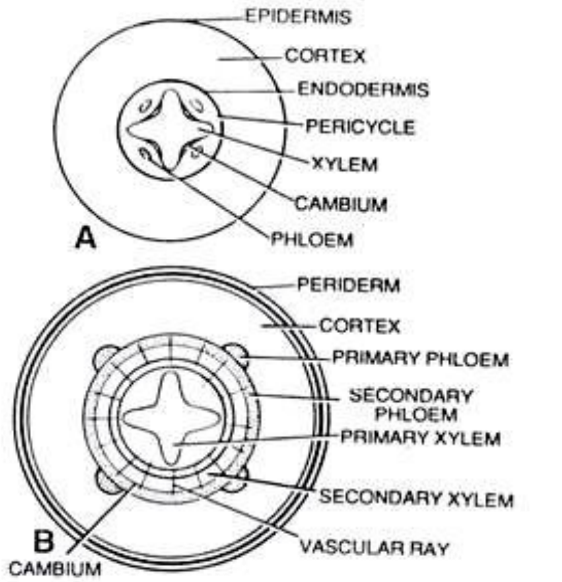


Fig. 42.44. Secondary growth in root A, cross section of a root without secondary growth; B, the same after considerable secondary growth.

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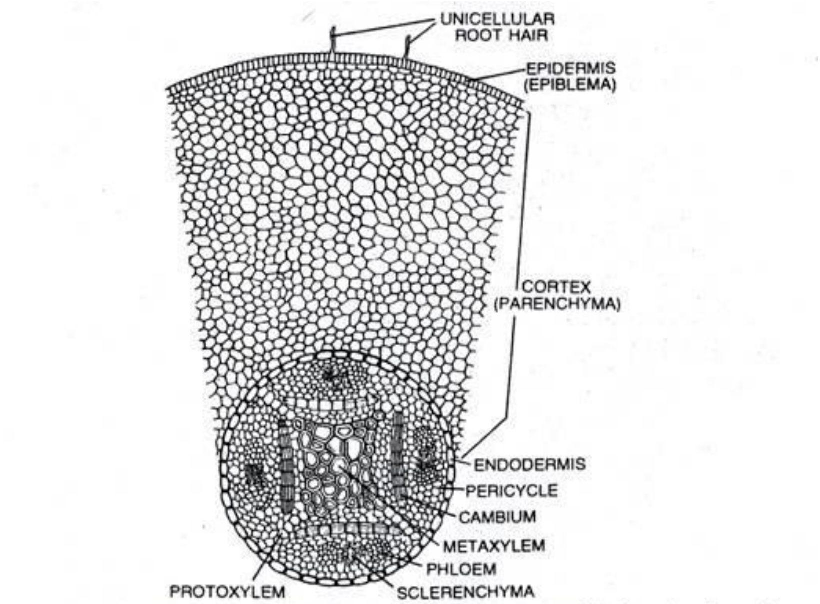

Fig. 42.45. The root. T.S. of gram root (dicot.) showing the beginning of the formation of cambium.

Now whole of the cambium ring becomes actively meristematic, and behaves in the similar way as in the stem, giving rise to secondary xylem on its inner side and secondary phloem towards outside.

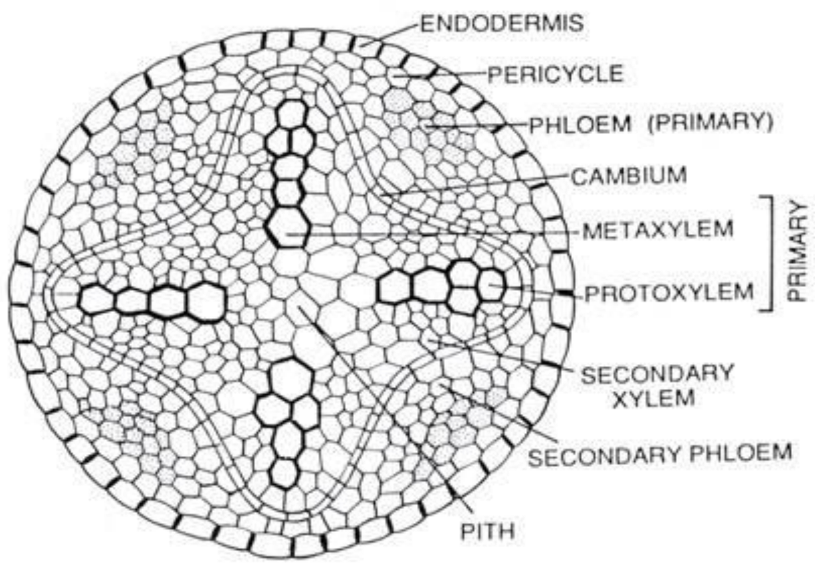

Fig. 42.47. Beginning of secondary growth in dicotyledonous root.

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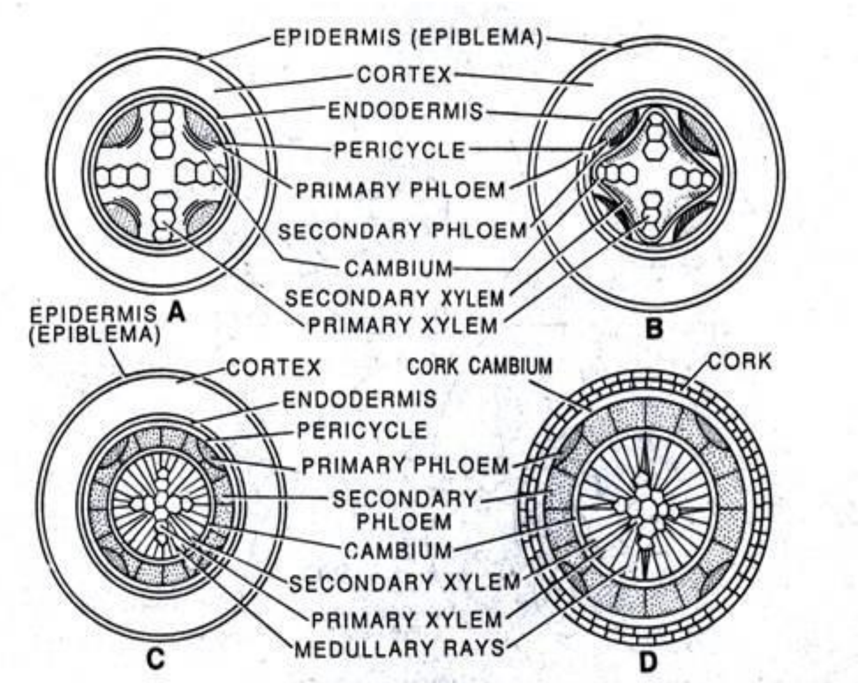

Fig. 42.48. Secondary growth in dicot root. A—D, diagrams showing stages in the secondary growth of a typical dicotyledonous root.

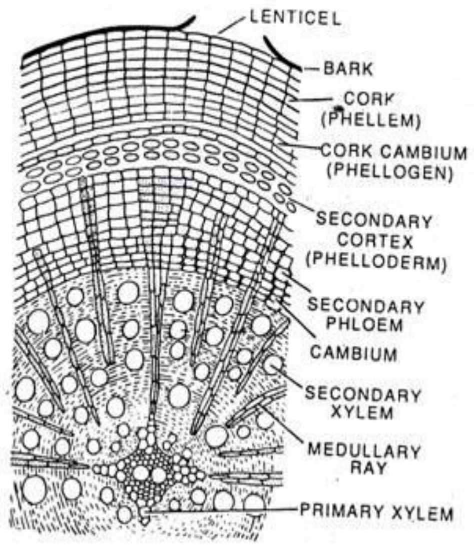

Fig. 42.49. Secondary growth. T.S. of dicotyledonous root showing secondary growth (later stage).

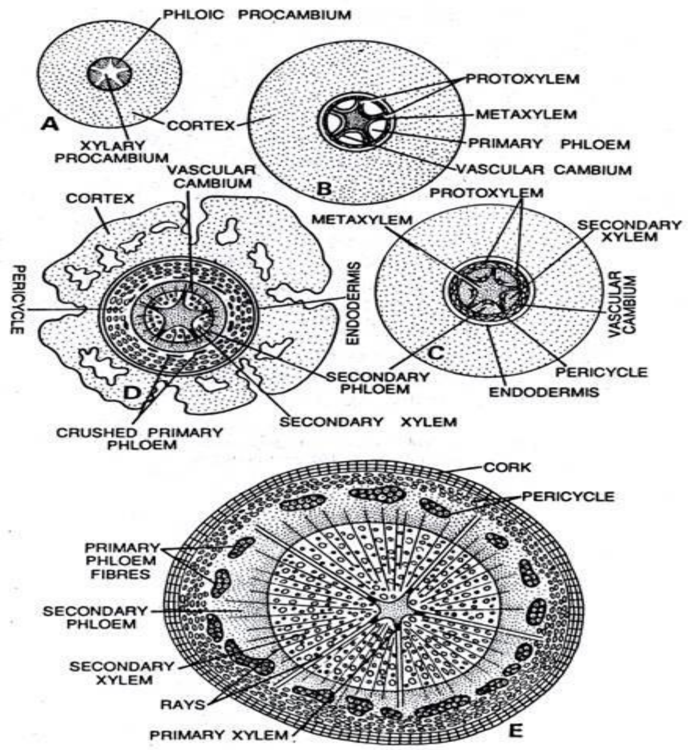

Fig. 42.50. The root. Secondary structure. Development of root in *Pyrus*.A, procambial state; B, primary growth completed; C, vascular cambium in between phloem and xylem produced some secondary vascular tissues; D, further secondary growth, pericycle increased in width by periclinal divisions; endodermis partly crushed cortex breaking down; E, further secondary growth, periderm developed, cortex has been shed. (After Esau.)

The secondary vascular tissues form a continuous cylinder and usually the primary xylem gets embedded in it. At this stage distinction can be made only by exarch primary xylem located in the centre. The primary phloem elements are generally seen in crushed condition.

The cambial cells that originate from the pericycle lying against the groups of protoxylem function as ray initials and produce broad vascular rays. These rays are traversed in the xylem and phloem through cambium; this is characteristic feature of the roots. Normally, such rays are called medullary rays.

Periderm : Simultaneously the periderm develops in the outer region of the root. The single layered pericycle becomes meristematic and divides, giving rise to cork cambium or **phellogen**. It produces a few brownish layers of cork cells or phellem towards outside, and the phelloderm on the inside.
The phelloderm does not contain chloroplasts. The pressure caused by secondary tissues ruptures the cortex with endodermis, which is ultimately sloughed off. The epiblema dies out earlier. Lenticels may also be formed.

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Stem. Secondary Growth in Dicot Stem

Primary growth produces growth in length and development of lateral appendages. Secondary growth is the formation of secondary tissues from lateral meristems. It increases the diameter of the stem. In woody plants, secondary tissues constitute the bulk of the plant. They take part in providing protection, support and conduction of water and nutrients.

Secondary tissues are formed by two types of lateral meristems, vascular cambium and cork cambium or phellogen. Vascular cambium produces secondary vascular tissues while phellogen forms periderm.

Secondary growth occurs in perennial gymnosperms and dicots such as trees and shrubs. It is also found in the woody stems of some herbs. In such cases, the secondary growth is equivalent to one annual ring, e.g., Sunflower.

A. Formation of Secondary Vascular Tissues:

They are formed by the vascular cambium. Vascular cambium is produced by two types of meristems, fascicular or intra-fascicular and inter-fascicular cambium. Intra-fascicular cambium is a primary meristem which occurs as strips in vascular bundles. Inter-fascicular cambium arises secondarily from the cells of medullary rays which occur at the level of intra-fascicular strips.

These two types of meristematic tissues get connected to form a ring of vascular cambium. Vascular cambium is truly single layered but appears to be a few layers (2-5) in thickness due to presence of its immediate derivatives. Cells of vascular cambium divide periclinally both on the outer and inner sides (bipolar divisions) to form secondary permanent tissues.

The cells of vascular cambium are of two types, elongated spindle-shaped fusiform initials and shorter isodiametric ray initials (Fig. 6.29). Both appear rectangular in T.S. Ray initials give rise to vascular rays.

Fusiform initials divide to form secondary phloem on the outer side and secondary xylem on the inner side (Fig. 6.28 B). With the formation of secondary xylem on the inner side, the vascular cambium moves gradually to the outside by adding new cells.

The phenomenon is called dilation. New ray cells are also added. They form additional rays every year (Fig. 6.28 D). The vascular cambium undergoes two types of divisions— additive (periclinal divisions for formation of secondary tissues) and multiplicative (anticlinal divisions for dilation).

Ray initials produce radial system (= horizontal or transverse system) while fusiform initials form axial system (= vertical system) of secondary vascular tissues.

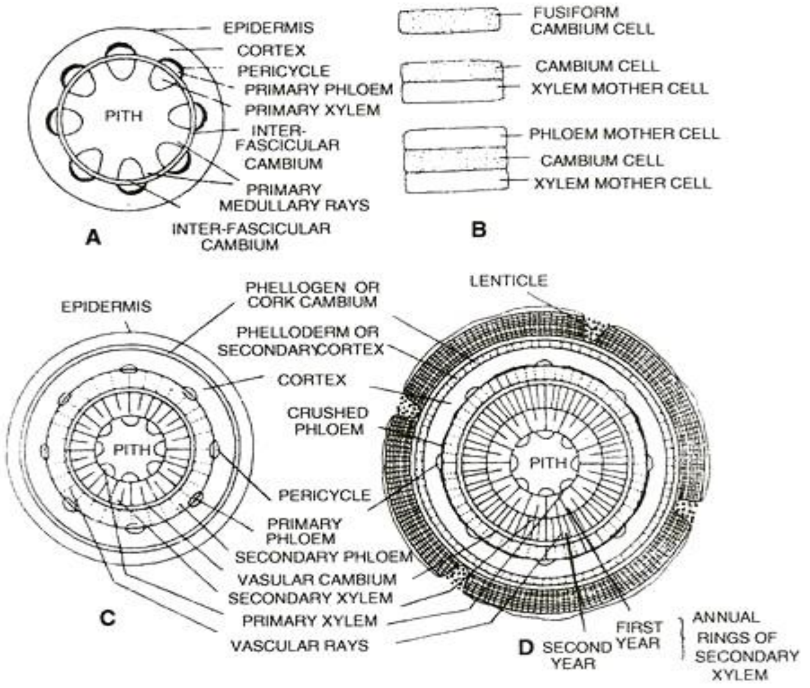

Fig. 6.28. A, complete ring of vascular cambium formed by strips of intrafascicular cambium and inter-fascicular cambium. B, formation of secondary vascular tissue mother cells; C, the beginning of secondary growth (mostly made up of secondary vascular tissues) of dicot stem (diagrammatic); D, two-year stage of secondary growth of a dicot stem.

1. Vascular Rays : The vascular rays or secondary medullary rays are rows of radially arranged cells which are formed in the secondary vascular tissues. They are a few cells in height.
Depending upon their breadth, the vascular rays are uniseriate (one cell in breadth) or multiseriate (two or more cells in breadth). Vascular rays may be homo-cellular (having one type of cells) or hetero-cellular (with more than one type of cells). The cells of the vascular rays enclose intercellular spaces.

The part of the vascular ray present in the secondary xylem is called wood or xylem ray while the part present in the secondary phloem is known as phloem ray. The vascular rays conduct water and organic food and permit diffusion of gases in the radial direction. Besides, their cells store food.

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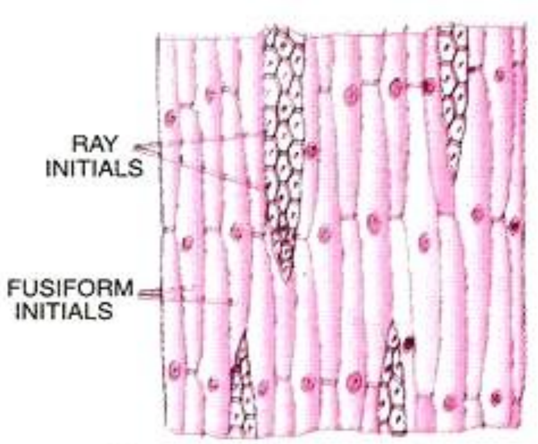

Fig. 6.29. L.S. Vascular cambium showing fusiform and ray initials.

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2. Secondary Phloem (Bast): It forms a narrow circle on the outer side of vascular cambium. Secondary phloem does not grow in thickness because the primary and the older secondary phloem present on the outer side gets crushed with the development of new functional phloem (Fig. 6.28 D). Therefore, rings (annual rings) are not produced in secondary phloem. The crushed or non-functioning phloem may, however, have fibres and sclereids.
Secondary phloem is made up of the same type of cells as are found in the primary phloem (metaphloem)— sieve tubes, companion cells, phloem fibres and phloem parenchyma.

Phloem parenchyma is of two types— axial phloem parenchyma made up of longitudinally arranged cells and phloem ray parenchyma formed of radially arranged parenchyma cells that constitute the part of the vascular ray present in the phloem.

Elements of secondary phloem show a more regular arrangement. Sieve tubes are comparatively more numerous but are shorter and broader. Sclerenchyma fibres occur either in patches or bands. Sclereids are found in many cases. In such cases secondary phloem is differentiated into soft bast (secondary phloem without fibres) and hard bast (part of phloem with abundant fibres).

3. Secondary Xylem : It forms the bulk of the stem and is commonly called wood. The secondary xylem consists of vessels, tracheids (both tracheary elements), wood fibres and wood parenchyma.
Wood parenchyma may contain tannins and crystals besides storing food. It is of two types— axial parenchyma cells arranged longitudinally and radial ray

parenchyma cells arranged in radial or horizontal fashion. The latter is part of vascular ray present in secondary xylem.

Secondary xylem does not show distinction into protoxylem and meta-xylem elements. Therefore, vessels and tracheids with annular and spiral thickenings are absent. The tracheary elements of secondary xylem are similar to those of meta-xylem of the primary xylem with minor differences. They are comparatively shorter and more thick-walled. Pitted thickenings are more common. Fibres are abundant.

Width of secondary xylem grows with the age of the plant. The primary xylem persists as conical projection on its inner side. Pith may become narrow and ultimately get crushed. The yearly growth of secondary xylem is distinct in the areas which experience two seasons, one favourable spring or rainy season) and the other un-favourable (autumn, winter or dry summer).

In favourable season the temperature is optimum. There is a good sunshine and humidity. At this time the newly formed leaves produce hormones which stimulate cambial activity. The activity decreases and stops towards the approach of un-favourable season. Hence the annual or yearly growth appears in the form of distinct rings which are called annual rings (Fig. 6.30).

Annual rings are formed due to sequence of rapid growth (favourable season, e.g., spring), slow growth (before the onset of un-favourable period, e.g., autumn) and no growth (un-favourable season, e.g., winter). Annual rings are not distinct in tropical areas which do not have long dry periods.

Fig. 6.30. Part of T.S. old stem showing annual rings.

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Annual Rings (Growth Rings). It is the wood formed in a single year. It consists of two types of wood, spring wood and autumn wood (Fig. 6.31). The spring or early wood is much wider than the autumn or late wood. It is lighter in colour and of lower density. Spring wood consists of larger and wider xylem elements.

The autumn or late wood is dark coloured and of higher density. It contains compactly arranged smaller and narrower elements which have comparatively thicker walls. In autumn wood, tracheids and fibres are more abundant than those found in the spring wood.

The transition from spring to autumn wood in an annual ring is **gradual** but the transition from autumn wood to the spring wood of the next year is **sudden**. Therefore, each year's growth is quite distinct. The number of annual rings corresponds to the age of that part of the stem. (They can be counted by increment borer).

Besides giving the age of the plant, the annual rings also give some clue about the **climatic conditions** of the past through which the plant has passed. Dendrochronology is the science of counting and analysing annual growth rings of trees.

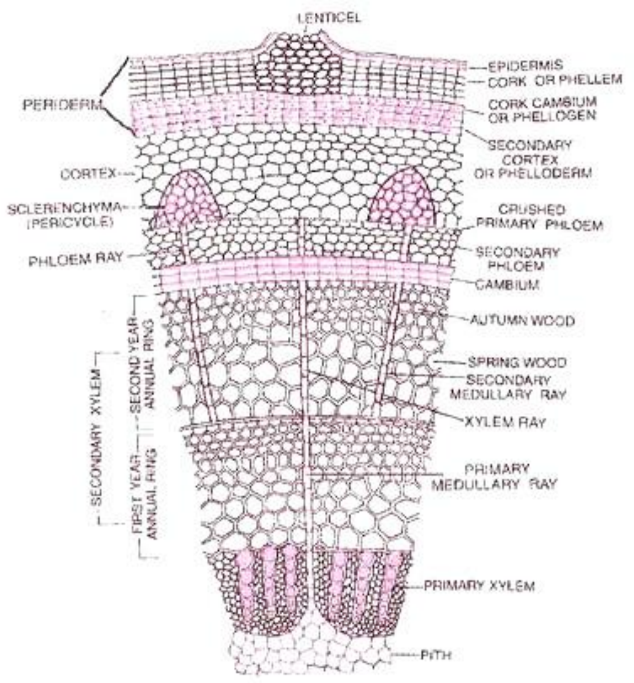

Fig. 6.31. Part of detailed structure of transverse section of two year old dicot stem showing secondary growth.

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Softwood and Hardwood :

Softwood is the technical name of gymnosperm wood because it is devoid of **vessels**. Several of the softwoods are very easy to work with (e.g., Cedrus, Pinus species). However, all of them are not 'soft'. The softness depends upon the content of **fibres and vascular rays**. 90-95% of wood is made of **tracheids and fibres**. Vascular rays constitute 5-10% of the wood.

Hardwood is the name of dicot wood which possesses abundant **vessels**. Due to the presence of vessels, the hardwoods are also called porous woods. In Cassia fistula and Dalbergia sissoo the vessels are comparatively very broad in the spring wood while they are quite narrow in the autumn wood. Such a secondary xylem or wood is called ring porous.

In others (e.g., Syzygium cumini Jambu) larger sized vessels are distributed throughout spring wood and autumn wood. This type of secondary xylem or wood is known as diffuse porous. Ring porous wood is more advanced than diffuse porous wood as it provides for better translocation when the requirement of the plant is high.

[The season after winter and before summer, in which vegetation begins to appear, in the northern hemisphere from March to May and in the southern hemisphere from September to November.
"in spring the garden is a feast of blossom"
Autumn, **season** of the year between summer and winter during which temperatures gradually decrease. It is often called **fall** in the United States because leaves **fall** from the trees at that time.]

Sapwood and Heartwood :

The wood of the older stems (dalbergia, Acacia) gets differentiated into two zones, the outer light coloured and functional sapwood or alburnum and the inner darker and nonfunctional heartwood or duramen (Fig. 6.33). The tracheids and vessels of the heart wood get plugged by the in growth of the adjacent parenchyma cells into their cavities through the pits. These ingrowths are called tyloses (Fig. 6.32).

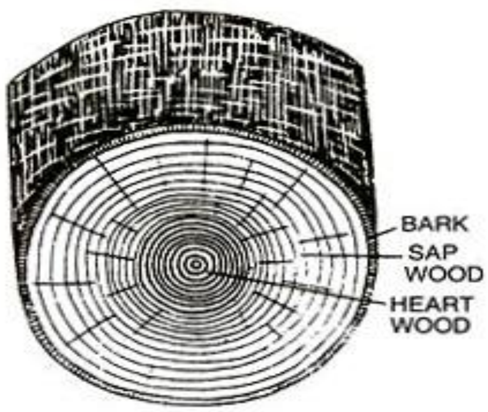

Fig. 6.33. Sapwood and heartwood in T.S. of trunk.

Ultimately, the parenchyma cells become lignified and dead. Various types of plant products like oils, resins, gums, aromatic substances, essential oils and tannins are deposited in the cells of the heartwood. These substances are collectively called extractives. They provide colour to the heartwood. They are also antiseptic. The heartwood is, therefore, stronger and more durable than the sapwood.

It is resistant to attack of insects and microbes. Heart wood is commercial source of Cutch (Acacia catechu), Haematoxylin (Haematoxylon campechianum), Brasilin (Caesalpinia sappan) and Santalin (Pterocarpus santalinus). Heartwood is, however, liable to be attacked by wood rotting fungi. Hollow tree trunks are due to their activity.

B. Formation of Periderm : In order to provide for increase in girth and prevent harm on the rupturing of the outer ground tissues due to the formation of secondary vascular tissues, dicot stems produce a cork cambium or phellogen in the outer cortical cells. Rarely it may arise from the epidermis (e.g., Teak, Oleander), hypodermis (e.g., Pear) or phloem parenchyma.
Phellogen cells divide on both the outer side as well as the inner side (bipolar) to form secondary tissues. The secondary tissue produced on the inner side of the phellogen is parenchymatous or collenchymatous. It is called secondary cortex or phelloderm. Its cells show radial arrangement.

Phellogen produces cork or phellem on the outer side. It consists of dead and compactly arranged rectangular cells that possess suberised cell walls. The cork cells contain tannins. Hence, they appear brown or dark brown in colour. The cork cells of some plants are filled with air e.g., Quercussuber (Cork Oak or Bottle

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Cork). The phelloderm, phellogen and phellem together constitute the periderm (Fig. 6.34).

Cork prevents the loss of water by evaporation. It also protects the interior against entry of harmful micro-organisms, mechanical injury and extremes of temperature. Cork is light, compressible, nonreactive and sufficiently resistant to fire.

It is used as stopper for bottles, shock absorption and insulation. At places phellogen produces aerating pores instead of cork. These pores are called lenticels. Each lenticel is filled by a mass of somewhat loosely arranged suberised cells called complementary cells.

Lenticels : Lenticels are aerating pores in the bark of plants. They appear on the surface of the bark as raised scars containing oval, rounded or oblong depressions (Fig. 6.34 A). They occur in woody trees but not in climbers. Normally they are formed in areas with underlying rays for facilitating gas exchange. Lenticels may occur scattered or form longitudinal rows.
A lenticel is commonly produced beneath a former stomate or stoma of the epidermis. Its margin is raised and is formed by surrounding cork cells. The lenticel is filled up by loosely arranged thin walled rounded and suberised (e.g., Prunus) or un-suberised cells called complementary cells (Fig. 6.34 B).

They enclose intercellular spaces for gaseous exchange. The complementary cells are formed from loosely arranged phellogen cells and division of sub-stomatal parenchyma cells. The suberised nature of complementary cells checks excessive evaporation of water.

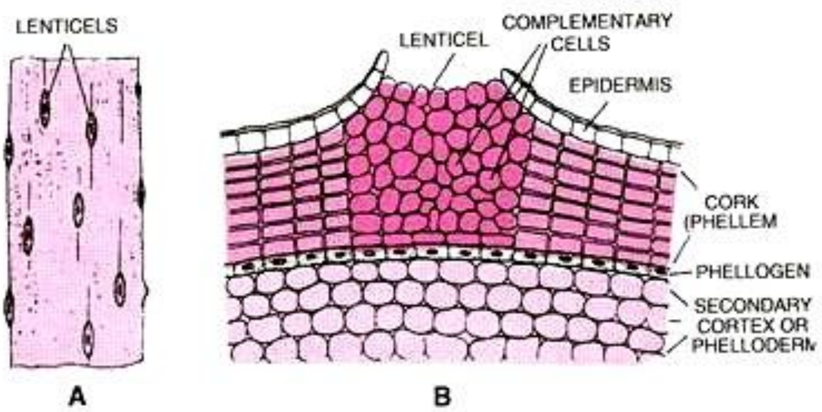


Fig. 6.34. Lenticels. A, external view of lenticels; B, T.S. lenticel.

In temperate plants the lenticels get closed during the winter by the formation of compactly arranged closing cells over the complementary cells.

Bark : In common language and economic botany, all the dead cells lying outside phellogen are collectively called bark. The outer layers of the bark are being constantly peeled off on account of the formation of new secondary vascular tissues in the interior. The peeling of the bark may occur in sheets (sheets or ring bark, e.g., Eucalyptus) or in irregular strips (scaly bark).
The scaly bark is formed when the phellogen arises in strips instead of rings, e.g., Acacia (vem. Kikar). Bark formed in early growing season is early or soft bark. The one formed towards end of growing season is late or hard bark.

Bark is insect repellent, decay proof, fire-proof and acts as a heat screen. Commercially it is employed in tanning (e.g., Acacia), drugs (e.g., Cinchona—quinine) or as spice (e.g., Cannamon, vem. Dalchini). The cork of Quercussuber is employed in the manufacture of bottle stoppers, insulators, floats, sound proofing and linoleum.

Significance of Secondary Growth:
1. Secondary growth adds to the girth of the plant. It provides support to increasing weight of the aerial growth.

2. Secondary growth produces a corky bark around the tree trunk that protects the interior from abrasion, heat, cold and infection.

3. It adds new conducting tissues for replacing old non-functioning ones as well as for meeting increased demand for long distance transport of sap and organic nutrients.

Anomalous Secondary Growth:
It is abnormal type of secondary growth that occurs in some arborescent monocots (e.g., Dracaena, Yucca, Agave) and storage roots (e.g., Beet, Sweet Potato). In arborescent monocot stems, a secondary cambium grows in hypodermal region. The latter forms conjunctive tissue and patches of meristematic cells. The meristematic patches grow into secondary vascular bundles.

Anomalous vascular bundles also occur in cortex (cortical bundles, e.g., Nyctanthes) and pith (e.g., Boerhaavia). In storage roots (e.g., Beet), accessory cambial rings appear on the outside of endodermis. They produce less secondary xylem but more secondary phloem. The secondary phloem contains abundant storage parenchyma.

Importance of Secondary Growth:

1. It is a means of replacement of old non-functional tissues with new active tissues.

2. The plants showing secondary growth can grow and live longer as compared to other plants.

3. It provides a fire proof, insect proof and insulating cover around the older plant parts.

4. Commercial cork is a product of secondary growth. It is obtained from Quercussuber (Cork Oak).

5. Wood is a very important product of secondary growth. It represents secondary xylem.

Axially and radially oriented elements;

1. Axial system. It consists of vertical files of tracheary elements.
The cells of **wood** are typically many times longer than wide, and are specifically **oriented** in two separate systems of cells: the **axial** system and the **radial** system. The cells of the **axial** system have their long axes running parallel to the long axis of the organ (e.g., up and down the trunk).

2. Radial system. It consists of rows of parenchymatous cells oriented at right angles to the longitudinal axis of the plant and forms **xylem rays or wood rays.** The height and thickness of xylem rays is revealed best in radial and tangential longitudinal sections respectively.

Types of rays

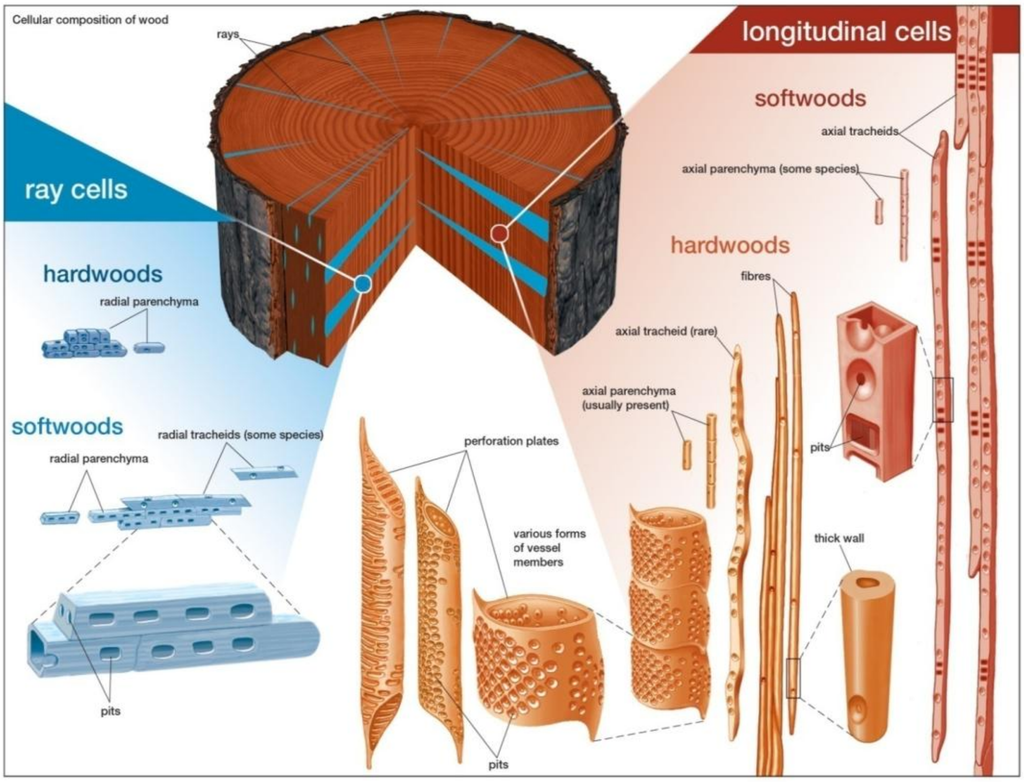
Ray (horizontal) tracheids are very short cells in comparison to **axial** tracheids (length 0.1– 0.2 mm) They have a general resemblance to **parenchyma** cells, but are different in that they are empty, tend (especially the marginal ones) to attain more irregular shapes, and possess small bordered pits.

Axial parenchyma;

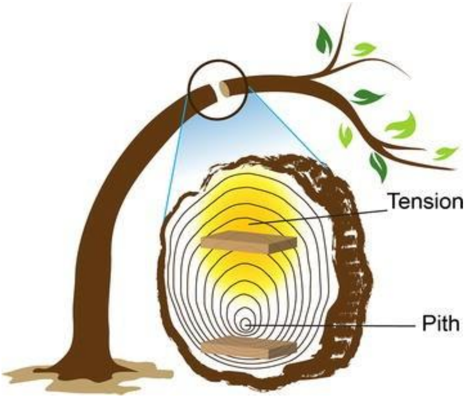
Distribution of the Axial Parenchyma

Axial parenchyma consists of axially elongate cells or (more commonly) strands of cells, alive at maturity, derived from fusiform cambial initials. **Axial parenchyma** cells are usually thinner-walled than the imperforate tracheary elements with which they are associated.

Cyclic aspects and reaction wood;



Reaction wood : In a woody plant is wood that forms in place of normal wood as a response to gravity, where the cambial cells are oriented other than vertically. It is typically found on branches and leaning stems. It is an example of mechanical acclimation in trees. Progressive bending and cracking would occur in parts of the tree undergoing predominantly tensile or compressive stresses were it not for the localised production of reaction wood, which differs from ordinary wood in its mechanical properties. Reaction wood may be laid down in wider than normal annual increments, so that the cross section is often asymmetric or elliptical. The structure of cells and vessels is also different, resulting in additional strength. The effect of reaction wood is to help maintain the angle of the bent or leaning part by resisting further downward bending or failure. There are two different types of reaction wood, which represent two different approaches to the same problem by woody plants:



In most angiosperms reaction wood is called **tension wood**. Tension wood forms on the side of the part of the plant that is under tension, pulling it towards the affecting force (upwards, in the case of a branch). It has a higher proportion of cellulose than normal wood. Tension wood may have as high as 60% cellulose.

Compression wood is a hard, dark-coloured **wood** typically found on the lower side of leaning stems and branches in conifers, Taxus and Ginkgo. This reaction **wood** is the result of the geotropic response of the tree, usually resulting from stem lean or the effect of stem flexing caused by wind.

Tension wood in dicots Compression wood in conifers

In gymnosperms and amborella it is called **compression wood**. Compression wood forms on the side of the plant that is under compression, thereby lengthening/straightening the bend. Compression wood has a higher proportion of lignin than normal wood. Compression wood has only about 30% cellulose compared to 42% in normal softwood. Its lignin content can be as high as 40%.
The controlling factor behind reaction wood appears to be the hormone auxin, although the exact mechanism is not clear. In a leaning stem, the normal flow of

auxin down the tree is displaced by gravity and it accumulates on the lower side. The formation of reaction wood may act in conjunction with other corrective or adaptive mechanisms in woody plants, such as thigomorphism (adaptive response to flexure) and gravitropism (the correction of, rather than the support of, lean) and the auxin-controlled balance of growth rates and growth direction between stems and branches. The term 'adaptive growth' therefore includes, but is not synonymous with, the formation of reaction wood.

As a rule, reaction wood is undesirable in any structural application, primarily as its mechanical properties are different from normal wood: it alters the uniform structural properties of timber. Reaction wood can twist, cup or warp dramatically during machining. This movement can occur during the milling process, making it occasionally dangerous to perform certain operations without appropriate safety controls in place. For instance, ripping a piece of reaction wood on a table saw without a splitter or riving knife installed can lead to kick back of the stock. Reaction wood also responds to moisture differently from normal wood.

Traditionally, compression wood does have niche applications. For instance, hunters in north Eurasia and the American Arctic were known to harvest compression wood for bow staves, because the increased density and compression strength of this wood enabled them to make functional weapons out of tree species that would otherwise be unsuitable for this purpose, due to their low strength and low density.

Sapwood and heartwood;

Two types of wood formation are prevalent in woody species after secondary growth – the outer nascent secondary xylem is the sap wood or alburnum, and the centrally placed older hard portion is referred to as heart wood or duramen. The former is light- colored containing some living cells in addition to the tracheary elements and fibres.

This part actually carries on the water and solute conduction in addition to mechanical support and storage of food. The hard central dark colored heart wood mainly consists of dead elements representing merely a solid mechanical column.

The sap wood is gradually transformed into heart wood through certain changes like:

1. The loss of protoplasts in the living cells.

2. Reduced water contents.

3. Withdrawal of the food matters from the cells.

4. Formation of tyloses to block the lumens of the tracheary elements.

5. Considerable lignifications of the walls of the parenchyma cells.

6. Infiltration of substances like gums, resins, oils and particularly tannins and coloring matters on both the walls and lumen of the elements.

Finally, the heart wood becomes more compact, strong and dark-colored. The heart wood is commercially more valuable than the sap wood but the latter is functionally more important. The heart wood yields good quality of timber due to its durability and resistance to decay. The dye haematoxylin is obtained from the heart wood of Haematoxylumcampechianum.

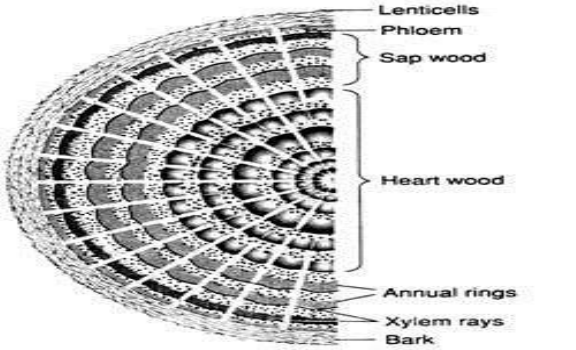


Fig. 5.134 : Secondary growth in stem in T.S. showing sap wood and heart wood

The living xylem elements of sap wood in course of time become dead and finally converted to heartwood. However, in Sequoia semper- virens the ray parenchyma of heart wood may remain alive for hundred years.

The ratio between the quantity and the degree of difference of heart wood and sap wood varies with different conditions of growth. In Abies, Picea etc. the heart woods are not well differentiated. Taxus and Morus possess thin sap wood while Fagus and Acer contain thick sap wood.

Ring and diffuse porous wood; **I**n **ring-porous trees**, the vessels laid down at the beginning of the growing season are much larger than subsequent vessels laid down at the end of the season. **Diffuse porous trees** form the vessel of roughly the same radial diameter throughout the growing season.

Ring Porous Wood and Diffuse Porous Wood.

Ring Porous Wood:

1. In it the vessels are of different diameter.

2. The vessels are not

3. Vessels with wide and smaller diameter are formed in the early and the later part of the growth season respectively.

4. Vessels with wide diameter of early wood and vessels of smaller diameter of late, summer or autumn wood are distinguishable.

5. The development of vessel is sudden and rapid.

6. The vessels are longer in length than those of diffuse porous wood.

7. The rate of transport of water in plant with ring porous wood is ten times faster than those with diffuse porous wood.

Diffuse Porous Wood:

1. In it the vessels are more or less equal in diameter.

2. The vessels are uniformly distributed throughout the wood.

3. Vessels with more or less equal diameter are formed throughout the growth ring.

4. Vessels of early wood and late wood are indistinguishable.

5. The development of vessel is slow.

6. The vessels are shorter in length than those of ring porous wood.

7. The rate of transport of water in plants with diffuse porous wood is slower than those with ring porous wood.

Early and late wood,

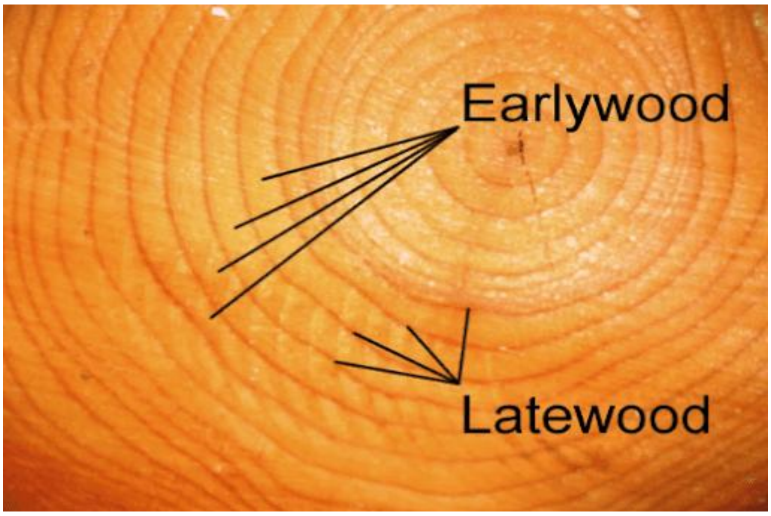
Early wood. The part of the **wood** in a growth ring of a tree that is produced earlier in the growing season. The cells of **early wood** are larger and have thinner walls than those produced later in the growing season.

Late wood. **Wood** in a growth ring of a **tree** that is produced **late** in the growing season and is harder and less porous than earlywood. Also called summerwood.

The process of **earlywood and latewood formation**, that is the frequency of division of cambial cells, the enlargement of newly **formed** xylem cells, and cell wall thicken are controlled by plant hormones. IAA is largely synthesized by buds in the tree crown, ... mainly to cambial cells and their differentiating cells.

Springwood and Summerwood (Autumnwood): Early and Late wood - The terms were originally applied to timbers of temperate region where there two distinct growth seasons-spring and summer. In India, in several localities, the growth activity does not always correspond to ordinary spring and simmer, hence the term are not strictly applicable. On the othere hand,there are trees, in which variable growth intensity is prominent;rapid growth in beginning of season in the form of thin walled cells followed by a slow growth of thick walled cells.The former may be called “earlywood” or “springwood” and the latter “latewood or summer/autumn wood,the former having a lighter shade of colour.Early wood part of the ring contains a large number of pores or vessels; is softer and more porous

[(Temperate having a moderate climate which especially lacks extremes in temperature)(The definition of tropical is the tropics - the warm, hot areas located between the Tropic of Cancer and the Tropic of Capricorn. Warm and humid weather often associated with the tropics is an example of tropical weather)].



Tyloses; **Tyloses** are outgrowths on parenchyma cells of xylem vessels of secondary heartwood. When the plant is stressed by drought or infection, **tyloses** will fall from the sides of the cells and "dam" up the vascular tissue to prevent further damage to the plant.

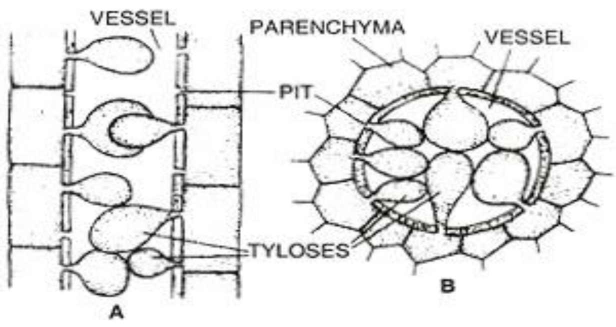


Fig. 6.32. Formation of tyloses in heartwood.
A, L.S. vessel showing tyloses.
B, T.S. vessel showing tyloses.

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Tylosoid : The epithelial cells in certain gymnosperms may block the resin duct by the enlargement and intrusions into them looking like tyloses, called the tylosoids (e.g., Pinus).
In angiosperm (e.g., Vitis, Bombax etc.) parenchyma proliferates into the neighboring sieve tubes in a tylose-like manner. These proliferations are also known as tylosoids. These tylosoids of gymnosperm and angiosperm differ from tyloses in not protruding through pits.

Dendrochronology. : Dendrochronology (or tree-ring dating) is the scientific method of dating tree rings (also called growth rings) to the exact year they were formed. As well as dating them this can give data for dendroclimatology, the study of climate and atmospheric conditions during different periods in history from wood.

Studying Dendrochronology

Dendrochronology is the study of data from tree ring growth. Due to the sweeping and diverse applications of this data, specialists can come from many academic disciplines. There are no degrees in dendrochronology because though it is useful across the board, the method itself is fairly limited. Most people who enter into studying tree rings typically come from one of several disciplines:

- Archaeology - for the purpose of dating materials and artefacts made from wood. When used in conjunction with other methods, tree rings can be used to plot events.
- Chemists - Tree rings are the method by which radiocarbon dates are calibrated.
- Climate Science - particularly in the field of palaeoclimatology where we can learn about the environmental conditions of the past, locally or globally, based on what the tree rings are telling us. By extension, this can also teach us about climate change in the future
- Dendrology - which also includes forestry management and conservation. Dendrologists are tree scientists and examine all aspects of trees
- Tree rings can tell them about the present local climate

In each growth season, trees create a new ring that reflects the weather conditions of that growth season. On its own, a single record can tell us only a little about the environmental conditions of the time in a specific year of the growth of the tree, and of course the age of the tree at felling, but when we put hundreds and thousands of tree-ring records together, it can tell us a lot more. Most importantly, assuming there are no gaps in the record (and even if there are short gaps), it can tell us the precise year that a certain tree ring grew .

Dendrochronology Defining Principles :

- Uniformity - that any individual tree ring record may be calibrated against the sum total of the existing record in order that it can be placed in the chronology. When calibrated, we should be able to tell precisely which year a certain ring was created
- Limiting factors - that certain weather and climate conditions have an effect on the tree ring growth in any given year or season
- Aggregation - The strength of the tree ring record is that variations for local conditions are taken into account and any tree ring data set should slot nicely into the existing record

- Ecological amplitude - Certain tree species will only grow in certain areas. Some like wet, salty soil and others prefer dry, acidic soil; there are preferences for temperature, humidity and most have an elevation limit. The best records are those taken from the margins of the land that the species prefer because it is here we see the most variations in tree ring growth

There is one major drawback to dendrochronology and that is that we can only date the rings in the tree. This says nothing about either when the particular tree was felled, nor about the date it was used. In past times, good quality timber may have been reused and for the archaeologist, it is important to check other records against the new data. Some trees are also better than others for study.

Notes on Reliability

Tree species vary greatly. In this article we make the assumption that growth is annual with a distinct growing season. Most tree species are reliable; oak is the most reliable tree type for tree rings - with not a single known case of a missing annual growth ring. Alder and pine are notorious for occasionally “missing a year” which is confusing enough without the fact that those species also sometimes “double up”, by having two rings in the same growth season.

A good dendrochronology study depends heavily on a lack of a repeated pattern. We expect, due to the changing nature of the climate, that each year will have a distinct pattern in the record. No pattern is likely to be repeated perfectly but it is certainly possible. All permutations must be examined and, if necessary, check the record against known external information.

Radiocarbon Dating

Part of the dendrochronological record is also to measure the amount of carbon in the tree sample, because of this lengthy record we will know the exact date that a tree ring was created inside the living organism. This ongoing record then, is vital to dating organic material through radiocarbon dating. The amount of radiocarbon-14 isotope in the artefact is compared against tree ring data for calibration, and it is always calibrated against organic material of known age. The comprehensive nature of the tree ring record is the perfect database against which to calibrate when we are trying to date organic materials. Most records will be unique and this should, in theory, give an absolute date for the artifact; if they have an identical level of the isotope,we can safely conclude that they are of the same age.

Uses in Archaeology : Sweet Track - it is known as “The Oldest Footpath in the World” which is a curious title not given out lightly.

Uses in Climate Studies : In the fight against climate change, it is to the past that we look in order to work out what our future might look like. The study of tree ring data is vital for understanding what our regional and global palaeoclimate looked like at any time, especially in light of the lack of other sources where we might get such information. The method has undergone immense improvement in the last 20 years. Where most climatologists look at how humans are affecting the climate, dendrochronology for climate science is focussed on the changes on vegetation that results from the natural processes of climate change **(16 p129-130)**. The method of change may have been different, but the results are the same and it can tell us much about increasing levels of carbon in the past. In this, it is vital to understanding what a post-climate change world will look like, particularly on trees, and the effects on tree growth in the future.

Annual Rings or Growth Rings: The secondary xylem in the stems of perennial plants commonly consists of concentric layers, each one of which represents a seasonal increment. In transverse section of the axis, these layers appear as rings, and are called annual rings or growth rings.
They are commonly termed as annual rings because in the woody plants of temperate regions and in those of tropical regions where there is an annual alternation of growing and dormant period, each layer represents the growth of one year.

The width of growth rings varies greatly and depends upon the rate of the growth of tree. Unfavorable growing seasons produce narrow rings, and favorable seasons wide ones. Annual or growth rings are characteristic of woody plants of temperate climates.

Such rings are weakly developed in tropical forms except where there are marked climate changes such as distinct moist and dry seasons. Annuals and herbaceous stems show, naturally, but one layer.

In regions with a pronounced cold season, the activity of the cambium takes place only during the spring and summer seasons thus giving rise the growth in diameter of woody plants. The wood of one season is sharply distinct from that of the next season. In spring or summer the cambium is more active and forms a greater number of vessels with wider cavities.

As the number of leaves increases in the spring season, additional vessels are needed for the transport of sap at that time to supply the increased leaves. In winter or autumn season, however, there is less need of vessels for sap transport, the cambium is less active and gives rise to narrow pitted vessels, tracheids and wood fibres.

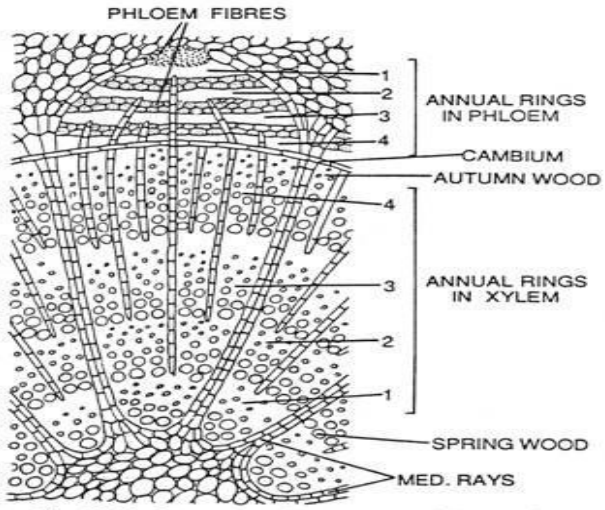

Fig. 40.42. Stem—secondary structure. Diagram of secondary thickening in a vascular bundle showing four annual rings.

The wood developed in the summer or spring season is called spring wood or early wood, and the wood formed in winter or autumn season is known as autumn wood or late wood. However, the line of demarcation is quite conspicuous between the late wood of one year and the early wood of next year. An annual ring, therefore, consists of two parts—an inner layer, early wood, and an outer layer late wood.

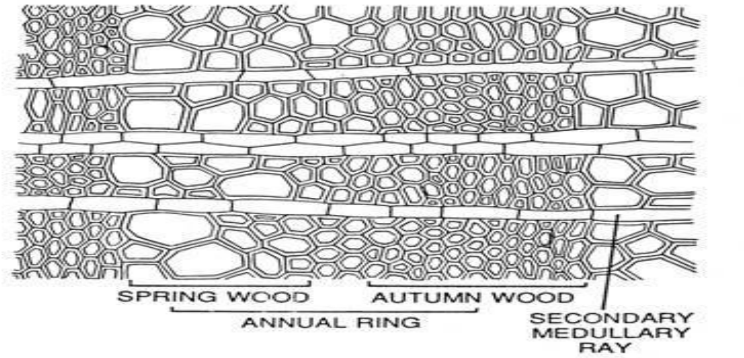

Fig. 40.43. Annual rings. An annual ring in sectional view (magnified).

Fig. 40.44. Annual rings (growth rings)—cut surface of a stem showing annual rings.

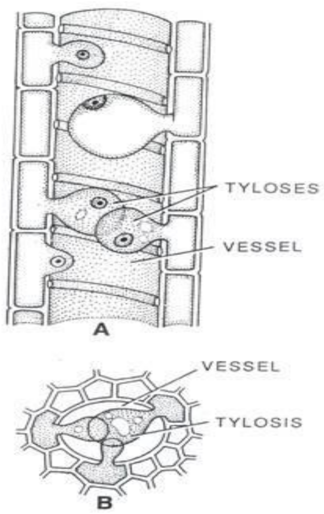

Fig. 40.45. Tyloses. A, L.S. of vessel with tyloses; B, T.S. of vessel with tyloses.

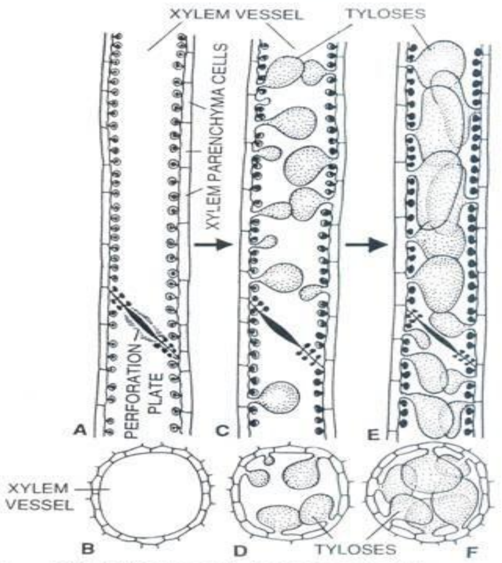

Fig. 40.46. Tyloses. A – F, development of tyloses in xylem vessels depicted in L.S. and T.S.

Dendrochronology:

Each annual ring corresponds to one year's growth, and on the basis of these rings the age of a particular plant can easily be calculated. The determination of age of a tree by counting the annual rings is known as dendrochronology.

Sometimes two annual rings are formed in a single year, and in such cases the counting of the annual rings does not show the correct age of the tree. This happens perhaps because of the drought conditions prevailed in the middle of a growing season.

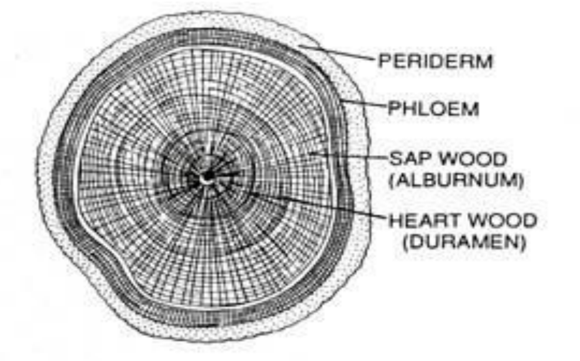

Fig. 40.47. T.S. branch of *Fraxinus*, showing heart and sapwood. (diagrammatic).

Development and composition of periderm, :Continued secondary growth in the interstellar region by the activity of the cambium cylinder large amount of pressure is exerted on the extrastelar tissues, which migrate ultimately to the epidermis.

As a result, the epidermis gets more stretched and ultimately tends to rupture exposing the internal tissues to the outside. In this situation, to protect the inner tissues, a new dermal tissue is formed secondarily, called periderm, in the extrastelar region.

It consists of three tissues:

1. A meristem known as phellogen or cork cambium.

2. The phellogen derived cells on the outer side, called phellem or cork cells.

3. The phellogen derived cells on the inner side, called phelloderm.

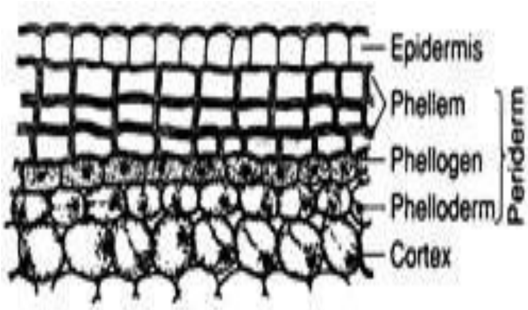

Fig. 5.136 : Diagram showing periderm formation

The phellogen or cork cambium is a secondary meristem arising from the living cells staying in the G_0 stage of the cell cycle.

It originates as a single layer of initiating cells either:

(a) In the sub epidermal portion, or

(b) In the epidermis itself,

(c) In the deep-seated layers of cortex or

(d) May even extend up to the phloem.

Phellogen consists of only one type of compactly arranged initials which appear rectangular in shape and flattened radially in transverse section. The cells divide tangentially producing new tissues in both centrifugal and centripetal directions. The derivatives usually remain arranged in radial rows.

The amount of phellem produced by the phellogen on the outer side is much more than that of phelloderm on the inner side. The cork cells or phellem are uniformly produced being arranged in distinct radial rows as they originate from a tangentially dividing meristem.

The cork cells are compactly arranged and have no intercellular spaces. After differentiation they become dead and become air-filled and accumulate coloring matters. The primary walls of these cells are mostly made of cellulose, partly suberin and lignin.

A thick layer of suberin is deposited next to the primary walls. So the cork cells become impervious to water and gases. In Eucalyptus the cork cells are extremely thick- walled and the cell lumens are completely filled up with resinous and other materials.

But usually they remain radially elongated, thin-walled empty cells. In Betula cork cell layer is peeled off like sheets of paper and the periderm serves as an effective secondary protective tissue against desiccation and mechanical injuries due to suberisation of the compactly arranged cork cells.

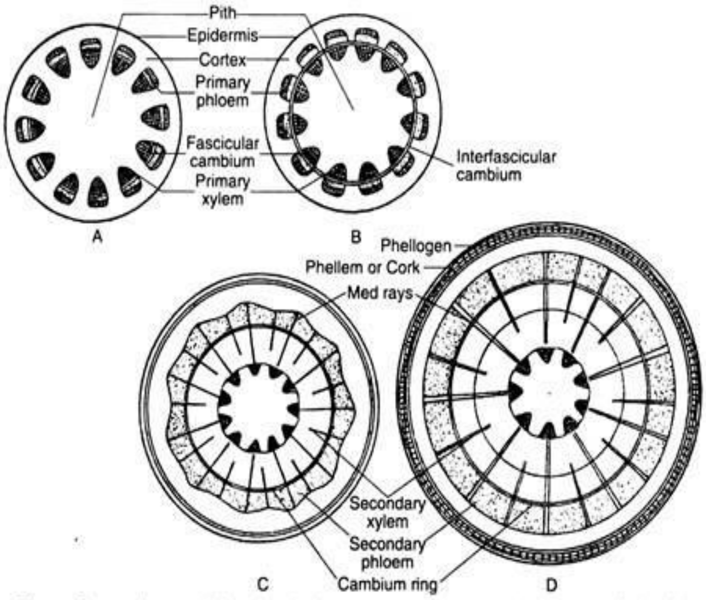

Fig. 5.138 : Stages of secondary growth in a dicotyledonous stem up to two years in diagrammatic view in transverse section

Table 5.15 : Difference between Cambium and Secondary Phellogen

	Cambium	Phellogen
1.	It is intrastelar in position.	It is extrastelar in position.
2.	Lying between xylem and phloem.	Lying external to the cortex.
3.	It is primary in origin.	It is secondary in origin.
4.	Procambium is the source of origin.	Epidermis, cortex or even phloem are the sources of origin.
5.	The cambial cells may be fusiform or isodiametric in shape.	The cork cambial cells may be polygonal or rectangular.
6.	It consists of fusiform initials and ray initials.	The cells are of single type.
7.	The cells may remain storied or non-storied in arrangement.	The cells are storied in arrangement.
8.	It produces secondary vascular and non-vascular tissues in the stele.	It produces non-vascular tissues outside the stele.
9.	It adds secondary phloem outside and secondary xylem inside.	It adds phellem outside and phellogen inside.
10.	It is also known as vascular cambium.	It is also known as cork cambium.

The phelloderm cells on the inner side resemble those of cortex.These cells are living, more or less isodiametric with intercellular spaces arranged in definite radial rows. They may photosynthesis and store food.

In conclusion, it can be said that secondary growth to increase in girth in a dicotyledonous stem is initiated in the intrastelar region by the activity of the cambium ring formed by the joining of the fascicular and interfascicular cambia and to cope up with pressure generated in the intrastelar region, periderm is formed in the extrastelar periphery.

What is the function of the periderm?

Although periderm may develop in leaves and fruits, its main function is to protect **stems** and roots. The fundamental tissues which compose the periderm are the phellogen, phelloderm, and phellem. The phellogen is the meristematic portion of the periderm and consists of one layer of initials.

rhytidome and : The **rhytidome** is the most familiar part of bark, being the outer layer that covers the trunks of trees. It is composed mostly of dead cells and is produced by the formation of multiple layers of suberized periderm, cortical and phloem **tissue**. The **rhytidome** is especially well developed in older stems and roots of trees.
Rhytidome is a special type of bark composed of successive layers of periderm as well as either the cortical parenchyma or secondary phloem. In Robinia periderm formation continues successively by the development of phellogen in the deeper regions of stem giving rise to periderm bands due to the death of the peripheral ones. The cork cells get suberised and the successive periderm bands enclose either cortical tissues or secondary phloem.

All the periderm bands together with the enclosed cortex or secondary phloem and all the tissues present external to the innermost phellogen are collectively referred to as rhytidome. The term bark is applied to all the tissues present external to the vascular cambium. Sometimes the term outer bark is applied to rhytidome and the living part of the bark inside the rhytidome is referred to as inner bark.

lenticels. : The secondary growth in thickness makes the epidermis to be replaced by the **periderm** in performing the protective function. The suberised walls of the dead cork cells are partly impervious to gases and thus for gaseous exchange between the internal living cells and the atmosphere some lens-shaped pores develop on the surface of the stem. These pores are known as lenticels. Only a few plants, mostly climbers, do not form lenticels though periderm is formed.

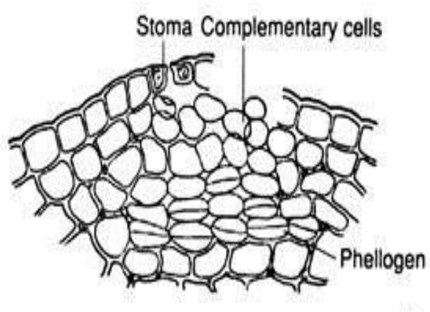

Fig. 5.139 : Early stages of formation of lenticel

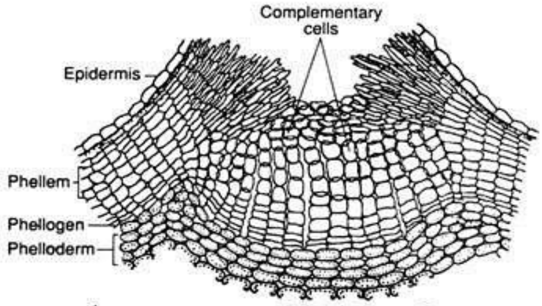

Fig. 5.140 : An well-developed lenticel in T.S.

Lenticel formation takes place for the first time just beneath the stomata present in the epidermis.

They usually start to form either:
(a) Just before the commencement of periderm formation, or

(b) Simultaneously with the periderm initiation, or

(c) After the initiation of the periderm.

The parenchyma cells adjacent to the substomatal chamber lose chlorophyll and divide in various planes to form a mass of colourless loose cells. Sooner or later normal phellogen is differentiated in the adjoining deeper region, which further produces loose cells on the outer side. The whole loose cell mass formed by the divisions in the sub-stomatal parenchyma as well as in phellogen on the outside is known as complementary cells.

With the continued addition of the complementary cell mass the epidermis is protruded above and finally ruptured, thus appearing like so many raised spots. The outermost cells at the atmospheric interface often die and are replaced by the cells derived from the phellogen. Often mass of compact cells, known as closing cells, alternate with loose complementary cells.

The closing cells together form a layer referred to as closing layer which helps to keep the loose complementary cells in position. During the active growing season the closing layer ruptures due to the pressure generated by the continued addition of the complementary cells. At the end of the growing season the closing layer is again formed.

The loose complementary cells are thin- walled, non-suberised with profuse intercellular spaces to establish communications with the internal tissues. Like the stomata the lenticels are thus mainly concerned with gaseous exchange between the atmosphere and the internal tissues.

In some cases, lenticels are formed in the stomata free regions. After the formation of the cork cells by the phellogen for a while loose complementary cells are produced in localised areas which ultimately protrude above and rupture through the cork giving rise to lenticels.

The number of lenticels formed in stem is variable. They may remain scattered or arranged in vertical or longitudinal rows. Rows of lenticels may occur opposite to the multiseriate rays, suggesting free interchange of gases between them.

Based on the orientation and rupture of the epidermis the lenticels may be transverse or longitudinal.

In dicotyledonous plants three types of lenticels are observed:
1. The complementary cells are suberised with little intercellular spaces as in Magnolia, Pyrus, Salix, etc.

2. Loose, non-suberised complementary cells followed by the formation of compact and suberized complementary cells as in Tilia,Quercus, etc.

3. Alternately arranged loose non-suberised complementary cells and compact suberised cells to form a multilayered complementary tissue as in Betula, Fagus, etc.

Bark : In large trees, due to continued formation of secondary tissues in the intrastelar region the periderm may not be adequate to withstand the inwardly generated pressure. In that case additional layers of periderm are formed successively in the deeper regions of the cortex, pericycle and even phloem. The outwardly cut-off phellem or cork cells by the phellogen ultimately get devoid of water and food supply and eventually become dead. All these dead tissues lying outside the active phellogen constitute the bark of the trees.

The term bark is loosely used and the term rhytidome is used for the outer bark covering all the tissues external to the innermost phellogen. Actually, the term bark is given to all tissues external to the vascular cambium.

Due to the formation of successive layers of periderm in the deeper regions of the stem the bark is formed in concentric rings surrounding the entire stem, which is known as ring bark. In some plants the periderm is formed as overlapping scale-like layers, known as scale bark. In Eucalyptus, Platanus, etc. the bark is intermediate between these two types, where the outer layers of the bark peel off in the form of sheets.

Polyderm: Polyderm is a special protective tissue consisting of twenty or more alternating layers of uniseriate suberised cells and multiseriate non- suberised cells. The peripheral cells are dead and the inner cells including the suberised cells contain living protoplasts. It is found in underground stems and roots of Rosaceae, Onagraceae, Myrtaceae and Hypericaceae.
At the time of its formation, a special phellogen is differentiated at the pericycle, which forms tissues by tangential divisions in centripetal succession. The newly formed tissues consist of thin walled non-suberised parenchyma cells alternating with uniseriateendodermoid cells.

The latter are differentiated into cork cells with the formation of casparian strips on their walls that later undergo more extensive suberisation. Polyderm is formed at the pericycle and it is exposed to outside after the death of the cortical tissues. It performs the function of protection of the inner living tissues. The non-suberised cells are concerned with food storage.

Table 5.16 : Difference between Periderm and Polyderm

	Periderm	Polyderm
1.	It is formed on the aerial stems and roots.	It is formed on the underground stems and roots.
2.	It is composed of phellem, phellogen and phelloderm.	It is composed of alternating layers of uniseriate endodermoid cells and multiseriate parenchyma.
3.	Suberin and sometimes lignin and wax are deposited.	Suberin is deposited on endodermoid cells.
4.	Casparian strips are not formed.	Casparian strips are formed before suberisation in endodermoid cells.
5.	The site of origin may be epidermis, hypodermis, cortex or phloem.	The site of origin is pericycle.
6.	The phellogen forms phellem outside and phelloderm inside.	The phellogen forms polyderm outside.
7.	Phellem cells differentiate into cork.	Endodermoid cells become cork due to suberization.
8.	The phellem and phelloderm are responsible for protection and storage of food respectively.	The outermost dead cells and non-suberized cells are responsible for protection and storage of food, respectively.
	Example : *Alistonia, Vitis, Clematis* etc.	Example : Rosaceae, Onagraceae etc.