SECONDARY GROWTH

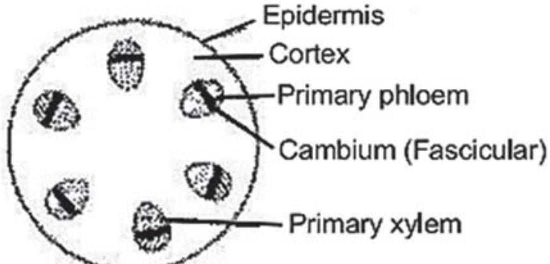
Before delving into the intricacies of secondary growth, it is essential to establish a clear understanding of primary and secondary growth. Primary growth refers to the lengthwise expansion of roots and stems, facilitated by apical meristems. On the other hand, secondary growth pertains to the increase in the girth or thickness of roots and stems, orchestrated by lateral meristems.

- **Primary Growth:** This involves the elongation of roots and stems through the activity of apical meristems. It is a fundamental aspect of plant development, contributing to the lengthening of plant structures. All plants undergo primary growth.
- **Secondary Growth:** In contrast, secondary growth focuses on the radial or girth expansion of roots and stems. While primary growth is universal, secondary growth is more characteristic of dicotyledonous plants. Monocots, generally lacking vascular cambium, tend to exhibit limited or no secondary growth.
- **Interfascicular Cambium:** One of the key players in secondary growth, this meristem occurs within vascular bundles.
- **Interfascicular Cambium:** This meristem forms between vascular bundles, contributing to the lateral growth of tissues.
- **Cork Cambium:** This lateral meristem is responsible for the production of cork cells, contributing to the protective outer layer of the stem.
- **Activation of Lateral Meristems:** Following the establishment of primary tissues, lateral meristems become active, initiating a process of cell division to generate secondary tissues. Secondary tissues encompass various components, including secondary xylem (wood), secondary phloem, secondary medullary rays, cork, and secondary cortex. Together, these tissues constitute the secondary body of many dicotyledons.
- **Secondary Growth in Gymnosperms:** Secondary growth is not exclusive to dicots; gymnosperms also undergo this process in their stems and roots. The involvement of lateral meristems, particularly cambium, results in the formation of additional vascular tissues and protective layers.

Secondary Growth in Dicot stem:

In the typical dicot stem, secondary growth unfolds through a series of distinct stages, significantly enhancing the girth and structural complexity of the plant. The key processes involved are as follows:

- **Formation of Cambial Ring:** Vascular bundles in dicot stems exhibit a characteristic 'ring' arrangement encircling the central pith. These bundles are termed open because they contain the cambium, also known as fascicular cambium or intrafascicular cambium. Initially present in patches as a single layer between the xylem and phloem in young stems, these intrafascicular cambia eventually amalgamate to form a continuous ring. Medullary rays, positioned between vascular bundles, play a pivotal role. When their cells undergo dedifferentiation, new cambium emerges, referred to as interfascicular cambium, situated between any two intrafascicular cambia. The combination of intrafascicular and interfascicular cambia constitutes the vascular cambial ring.



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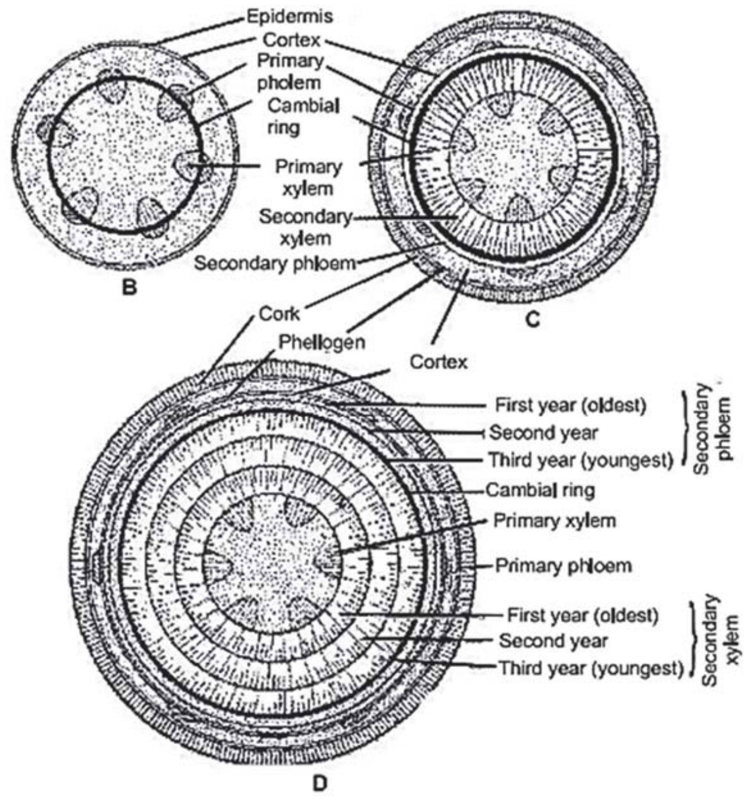

Fig. : Stages of secondary growth in a woody (dicot) stem; stages in transverse views

- **Activity of the Cambial Ring:** The established cambial ring becomes active, initiating divisions that result in the formation of new cells both inward and outward through periclinal divisions. Given the arrangement of xylem toward the pith and phloem toward the periphery within a vascular bundle, cells severed by the cambial ring toward the pith mature into secondary xylem, while those cut off toward the periphery develop into secondary phloem.
  The cambium exhibits greater activity on the inner side, leading to a more substantial production of secondary xylem compared to secondary phloem. Consequently, the cambium ring expands toward the periphery.
  The continuous formation and accumulation of secondary xylem exert pressure on the primary and secondary phloem, causing them to gradually collapse and become obliterated. Meanwhile, primary xylem remains relatively intact, often located in or around the center.
  This progression results in the separation of primary xylem and primary phloem, which were initially closer together.
- **Secondary Medullary Rays:** In certain areas, the cambium gives rise to a slender band of parenchyma extending radially through the secondary xylem and secondary phloem. These bands, known as secondary medullary rays or vascular rays, manifest as continuous strips bridging secondary xylem and secondary phloem. Radially arranged, these rays serve as conduits for the transport of food, water, and minerals from the center to the periphery of the organ. They play a crucial role in facilitating the exchange of essential substances during plant growth and development.

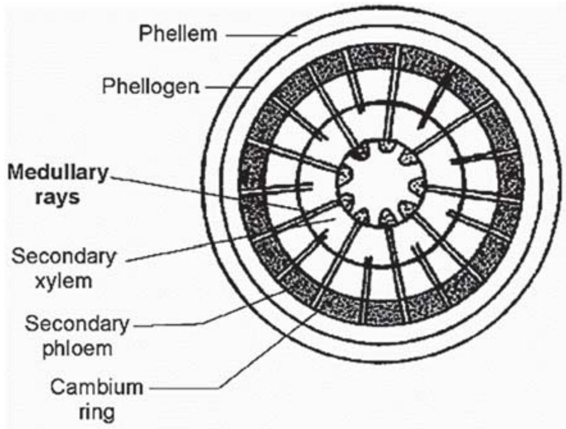

Fig. : T.S. of a dicot stem showing medullary rays

Growth Rings or Annual Rings (Springwood and autumn wood):

The formation of growth rings or annual rings, a phenomenon observed in the secondary xylem of plants, is intricately linked to the dynamic activity of the cambium ring, which is responsive to both external climatic variations and the internal environment of the plant.

- **Seasonal Variation in Secondary Xylem:** In regions characterized by temperate climates such as Asia and Central North America, the climate undergoes marked variations across different seasons. These fluctuations profoundly influence the activity of the cambium, leading to the production of distinct types of secondary xylem in various seasons.
- **Springwood and autumn wood Formation:** During the spring season, the cambium exhibits heightened activity, giving rise to a significant number of xylary elements, including vessels, tracheids, xylem fibers, and xylem parenchyma. Vessels, characterized by wider lumens, are particularly abundant as they cater to the increased water demand resulting from an expanded transpiring surface. This wood formed in spring is termed springwood or early wood. Conversely, in the winter, the cambium's activity diminishes, resulting in the formation of fewer xylary elements. Vessels produced during this period have narrower lumens due to reduced water needs. The wood generated in winter is known as autumn wood or latewood.
- **Characteristics of Springwood and autumn wood:** Springwood is lighter in color and possesses lower density, while autumn wood exhibits a darker hue and higher density.
- **Annual Ring Formation:** The transition from springwood to autumn wood occurs gradually, whereas the shift from autumn wood to springwood is abrupt. This alternation between springwood and autumn wood, appearing as concentric rings with alternating light and dark colors, constitutes an annual ring. Each annual ring comprises one circle of springwood and one circle of autumn wood. The term "annual ring" reflects the representation of one year's growth, and it is also referred to as a "growth ring" due to its continuous increase with ongoing plant growth.
- **Dendrochronology:** The distinctness of annual rings in a cut stem provides a valuable tool for estimating the age of a tree. Each annual ring corresponds to one year of growth, allowing researchers to determine the tree's age by counting these rings in the transverse section of the stem. This study is known as dendrochronology.
- **Geographic Variability of Annual Rings:** While annual rings are clearly discernible in plants from temperate regions, they do not develop in plants thriving in areas characterized by uniform temperature and rainfall throughout the year, such as tropical regions. In such environments, the consistent activity of the cambium results in the formation of a uniform secondary xylem, devoid of the distinct characteristics observed in plants experiencing seasonal variations.

- **Heartwood and Sapwood:** As a tree undergoes prolonged secondary growth over several years, a significant transformation occurs in the composition and functionality of its secondary xylem, resulting in the distinct regions known as heartwood and sapwood. This process is particularly noticeable in the older segments of the stem, primarily concentrated in the central or innermost layers.

  Changes in Secondary Xylem: Over the course of the tree's maturation and continuous secondary growth, the majority of its secondary xylem, commonly referred to as wood, undergoes a color transformation, turning into a deep brown shade. This alteration becomes more evident in the stem's older sections.

  Deposition of Organic Compounds: The darkening of color in the central layers is attributed to the gradual accumulation and deposition of various organic compounds such as tannins, resins, oils, gums, aromatic substances, and essential oils within the vessels and tracheids of the aging secondary xylem.

  Formation of Heartwood: This accumulation of organic substances leads to the obstruction of xylary elements, specifically vessels and tracheids, rendering them non-functional in terms of water conduction. Despite losing its primary role as a conductive tissue, this modified and inert inner secondary xylem is designated as heartwood (duramen). Heartwood consists of deceased elements characterized by highly lignified cell walls, offering durability and resistance against microbial and insect attacks.

  Tyloses in Heartwood: Heartwood is known for the presence of tyloses or tracheal plugs, which are balloon-like protrusions formed by the swelling of xylem parenchyma cells into the vessels' lumens. These tyloses contribute to the non-functionality of the vessels in heartwood.

  Mechanical Support and Loss of Conductivity: While heartwood does not serve as a conduit for water, it plays a crucial role in providing mechanical support to the stem. The deposition of organic compounds fortifies the heartwood, enhancing its resistance to external threats.

  Sapwood and Water Conduction: In contrast, the peripherally located younger regions of the secondary xylem, referred to as sapwood (alburnum), maintain a lighter color. Sapwood actively participates in the conduction of water and minerals from the roots to the leaves in mature trees.

  Transition from Sapwood to Heartwood: With the passage of time and the addition of new outer rings of secondary xylem, the sapwood undergoes a gradual transition into heartwood. This transformation occurs as successive rings of sapwood are converted into heartwood, maintaining the overall thickness of the sapwood.

  The symbiotic roles of heartwood and sapwood showcase the dynamic adaptation of tree anatomy to ensure both structural integrity and the efficient transport of water and minerals in the plant's life cycle.

Activity of Cork Cambium:

- **Stimulation of Cork Cambium:** The continuous activity of vascular cambium fuels the perpetual increase in the stem's girth during secondary growth. However, this relentless expansion results in the rupture of the outermost layer, including the epidermis and outer cortical layers of the stem. To counteract this rupture and provide renewed protection, a secondary lateral meristem known as cork cambium, or phellogen, comes into play. The cork cambium typically develops within the cortex region.
- **Extra-Stelar Origin of Cork Cambium:** Originating outside the stele, the cork cambium is alternatively termed the extra-stelar cambium. The stele encompasses all tissues on the inner side of the endodermis, comprising pericycle, vascular bundles, and pith.
- **Phellogen Structure and Differentiation:** The phellogen consists of two layers of meristematic cells, characterized by their thin-walled and nearly rectangular shape. The outer cells of the phellogen undergo differentiation to form cork or phellem, while the inner cells differentiate into secondary cortex or phelloderm.
- **Cork or Phellem:** Initially, cork cells are tightly packed and possess thin cellulosic walls. As these cells mature, a gradual loss of living matter occurs, accompanied by the thickening of cell walls due to the

deposition of a fatty substance known as suberin. The suberin-laden cell walls render cork impervious to water.

- **Phelloderm:** Functioning as the secondary cortex developed during secondary growth, phelloderm comprises living cells with thin-walled parenchymatous cells, featuring cellulosic cell walls.
- **Formation of Periderm:** Collectively, phellogen, phellem, and phelloderm constitute the periderm. These layers collectively grow following the rupture of the primary plant body's epidermis and outer cortical layers. Therefore, the secondary growth in the cortex facilitated by cork cambium is a consequence of the secondary growth initiated by vascular cambium, which induces the need for replacement.
- **Pressure Build-Up and Bark Formation:** The continuous activity of cork cambium exerts pressure on the layers peripheral to phellogen. Over time, the layers adjacent to phellogen undergo death and slough off, relieving the built-up pressure.
- **Composition of Bark:** The entirety of tissues outside the vascular cambium constitutes the bark, encompassing periderm (phellogen, phellem, and phelloderm), primary cortex, pericycle, primary and secondary phloem. These tissues reside outside the vascular cambium.
- **Bark Development and Lenticels:** Bark formed earlier in the season is referred to as early or soft bark, whereas that formed toward the season's end is termed late or hard bark. Lenticels, small portions of periderm resulting from phellogen activity, serve as openings on the bark's surface. When phellogen activity intensifies at a specific point, it produces loosely arranged, thin-walled parenchymatous cells-complementary cells-instead of the typical thick-walled cork cells. The increased number of complementary cells exerts pressure on the epidermis, leading to its rupture. These openings, termed lenticels, assume a lens-shaped appearance.

Fig: Bark

- **Lenticels' Role as Breathing Pores:** Lenticels play a crucial role as breathing pores, facilitating the exchange of gases between the internal tissues of the stem and the external atmosphere. Found in most woody trees, lenticels enable gas exchange in the woody areas of plants and may also contribute to water loss in the form of vapors. Therefore, lenticels are alternatively referred to as breathing pores.

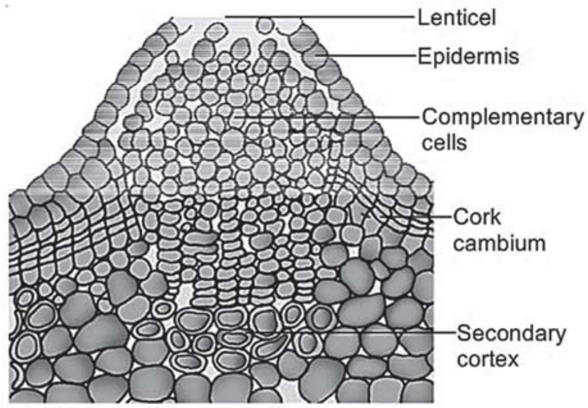

Fig. : Lenticel

Secondary Growth in Dicot Roots:

Similar to dicot stems, dicot roots also undergo secondary growth, leading to an increase in girth. This growth is facilitated by the activity of two lateral meristems, namely vascular cambium and cork cambium. Notably, the vascular cambium is not initially present in dicot roots but develops later during secondary growth. The secondary growth process in dicot roots can be outlined as follows:

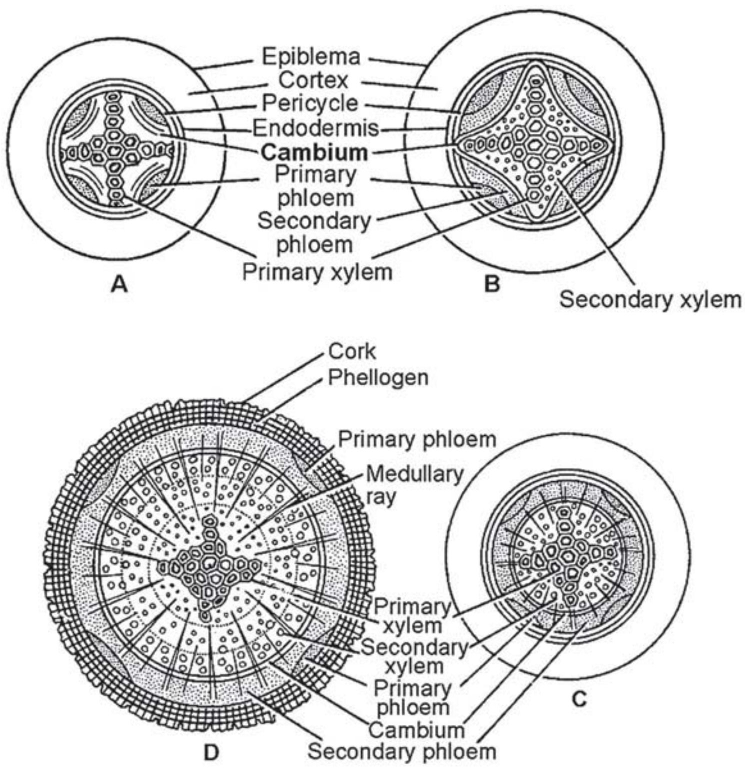

Fig. : Different stages in secondary growth of dicot root

- **Origin and Activity of Vascular Cambium:** In dicot roots, the arrangement of vascular bundles is radial, and the xylem is exarch. Unlike dicot stems, the vascular cambium is absent initially and forms later during secondary growth. This makes the vascular cambium entirely secondary in origin. Various tissues contribute to the formation of vascular cambium. In the radial arrangement, xylem and phloem tissues are aligned along different radii alternately. Consider a tetrarch root as an example, where four distinct patches of primary xylem and four patches of primary phloem are present.

Initially, the parenchyma cells just below the primary phloem (towards the pith) become meristematic, giving rise to four separate strips of cambia (matching the four phloem patches in a tetrarch root). Initially, these cambia strips are separate and have not formed a continuous ring. Subsequently, divisions of pericycle cells lead to the formation of a complete cambial ring. Only those pericycle cells above the protoxylem divide and contribute to the formation of the cambium ring, resulting in a complete and continuous wavy cambial ring.

The wavy ring exists below the phloem but above the xylem. The cambia strips cut off cells on both sides, with cells toward the inner side maturing into secondary xylem and those on the outer side maturing into secondary phloem. This wavy ring gradually becomes circular, cutting off secondary xylem internally and secondary phloem externally.

The vascular cambium is entirely secondary in origin in dicot roots, originating from the tissue just below the phloem bundles and a portion of pericycle tissue above the protoxylem, forming a complete and continuous wavy ring that later becomes circular.

Following stelar secondary growth, a central cylinder of wood (secondary xylem) surrounded by secondary phloem is formed.

- **Origin and Activity of Cork Cambium (Phellogen):** Cork cambium, another meristematic tissue, arises from divisions of pericycle cells. Cork cambium gives rise to periderm, which comprises protective cell layers to replace the ruptured epidermis and outer cortical layers.

  The activity of cork cambium in dicot roots mirrors that found in dicot stems. It produces cork cells on the outer side and secondary cortex on the inner side. Cork cells, rich in suberin in their walls, become dead due to further suberin deposition. Cork cambium's activity results in pressure building up on the remaining layers peripheral to phellogen (cork cambium), namely the primary cortex and epidermis. Eventually, these layers die and slough off.