Secondary Growth

Objectives

After going through this lesson, the learners will be able to understand the following:

- Secondary Vascular Growth
- Permanent Tissues
- Heart Wood and Sap Wood

Content Outline

- Introduction
- Secondary Vascular Growth
  - Secondary Vascular Growth in Stem
- Heart Wood and Sap Wood
- Summary

Introduction

A plant not only grows in length but also in girth (diameter). The growth in length, also known as the primary growth, is the result of activity of apical meristems which are located at the root and shoot apices. The increase in girth or diameter is because of the production of secondary tissues by the activity of **lateral meristems**. This growth is, thus, known as secondary growth. In general, secondary growth is present in most dicots but absent in all monocots (except in some which exhibit an anomalous type of secondary growth). It is absent or of limited presence in some herbaceous dicotyledonous species. A few dicotyledonous species exhibit abnormal or anomalous secondary growth.

There are two types of lateral meristems, the **vascular cambium** and the **cork cambium**. Whereas activity of vascular cambium produces secondary vascular tissues and increases the thickness of vascular tissues to meet the increasing requirement of the growing plant for water, minerals and food, the activity of cork cambium, also called as **phellogen** results in formation of secondary cortex and cork tissue (secondary ground tissue/**periderm**) outer to the vascular tissues to replenish the outer layers of dead and injured cells which get periodically sloughed off with increasing girth. Both, vascular and cork cambium, possess highly vacuolated cells which are cuboidal in shape.

Secondary Vascular Growth

Mitotic activity in cells of vascular cambium produces secondary vascular tissues in both stem and root. Normally, cells cutoff by vascular cambium toward the inner side or centre of the organ differentiate into secondary xylem and those cutoff toward the outer side differentiate into secondary phloem. Once formed, the vascular cambium in stem and root remains active for the entire life of the plant. However, the origin and development of vascular cambium in the two organs is somewhat different.

Secondary Vascular Growth in Stem:

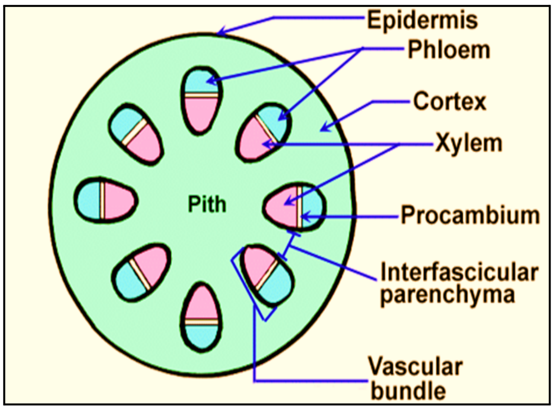
Generally, secondary vascular growth is exhibited by stems possessing open vascular bundles. Open vascular bundles contain cambium cells (remnants of procambium of embryo) between the xylem and phloem tissues. In herbaceous species this cambium stops dividing and differentiates into xylem and phloem. Inwoody species, however, the cambium retains the ability to divide and forms the **intrafascicular cambium** (also called fascicular cambium).

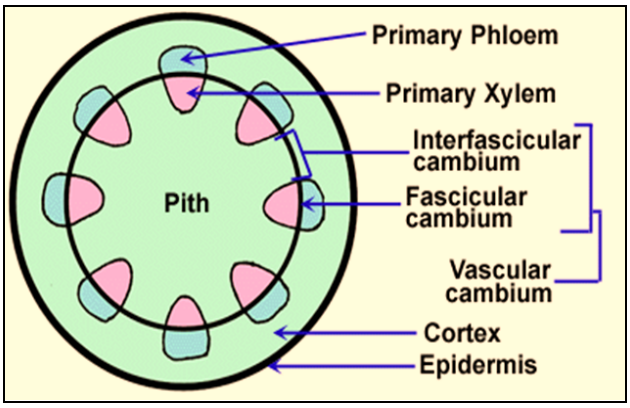
Initiation of secondary growth occurs through activation of intrafascicular cambium which cuts off secondary xylem toward the inside and secondary phloem toward outside of the organ. Subsequently, parenchyma cells of medullary rays present between the intrafascicular cambium of neighbouring vascular bundles become meristematic and form the **interfascicular cambium**. These connect on each side with fascicular cambia forming a complete cylinder of vascular cambium. This cylinder of vascular cambium then cuts off a cylinder of secondary xylem toward inside and secondary phloem toward outside. In any year, both xylem and phloem are produced but almost always much more xylem than phloem is formed. Because of the pressure from the continuous expansion of secondary vascular tissues, the outer phloem layers get crushed.

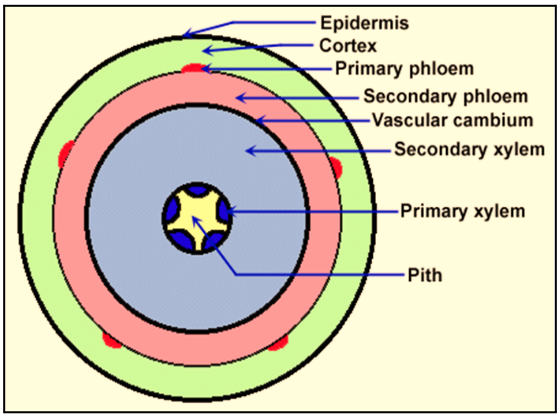
The vascular cambium is made up of two types of cells: the **fusiform initials** and the **ray initials**. Fusiform initials are vertically elongated long tapering cells. They divide to produce elongated cells of secondary xylem, viz. tracheids, vessel elements and xylem fibres, as well as of secondary phloem, viz. sieve tube members, companion cells and phloem fibres.

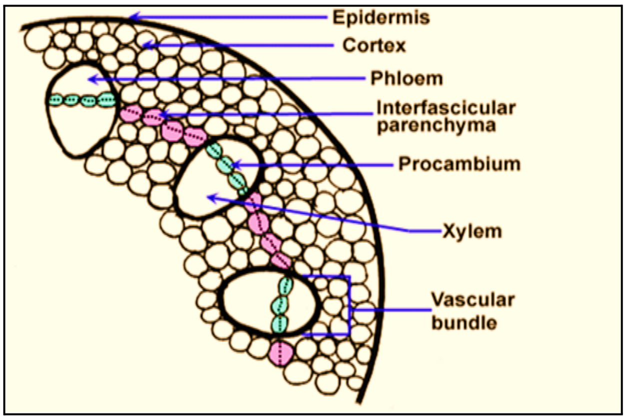
The ray initials are short horizontally (radially) elongated cells that produce ray parenchyma cells. These cells pass through secondary xylem and secondary phloem in a radial direction and form the **secondary medullary rays**. Ray cells are involved in short distance horizontal conduction of sap, and in storage of substances such as starch, proteins, fats, and crystals etc.

Secondary xylem, commonly known as wood, is mostly made up of tracheids, vessels, and fibres which are lignified and dead cells. Thus, in addition to conducting water and minerals etc, the lignified cells of the wood also provide support for the growing plant.









Spring Wood and Autumn Wood

The activity of vascular cambium does not remain uniform throughout the year but fluctuates. A number of environmental and physiological factors affect it. In temperate regions, during autumn and winter seasons, the temperatures are low and the water available to the plant in the ground decreases. Under such conditions, cambium activity decreases. The secondary xylem produced is less and contains cells with narrower lumen and thicker walls.

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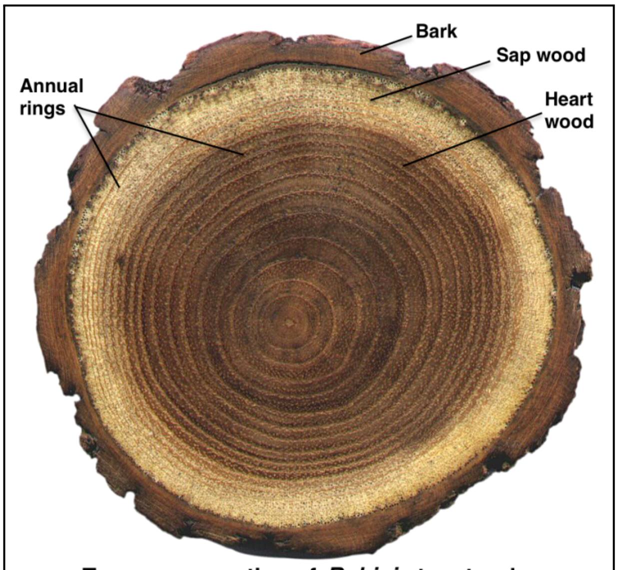
to the plant in the ground decreases. Under such conditions, cambium activity decreases. The secondary xylem produced is less and contains cells with narrower lumen and thicker walls. Such wood has more fibres, is denser and appears darker. It is called the **autumn / winter wood** or **late wood** as it forms in the latter part of the growing season of the plant.

But in the spring and summer when temperatures rise and more water becomes available, cambium activity increases; it forms more xylem with larger thin-walled (wider lumen) cells. This wood also has fewer fibres. It looks lighter and is called
spring / wood or **early wood**.

Wood of one year or growing season, consisting of the light-coloured early wood and the dark-coloured late wood, forms one **annual ring** or **growth ring**. The growth rings are distinct if the differences in the early and late wood are conspicuous, and are often used to determine the age of a tree. **Dendrochronology** is the science of dating based on the study of growth rings of trees.



Transverse section of *Robinia* tree trunk

Source:https://upload.wikimedia.org/wikipedia/commons/9/98/Robinia_sezione.png

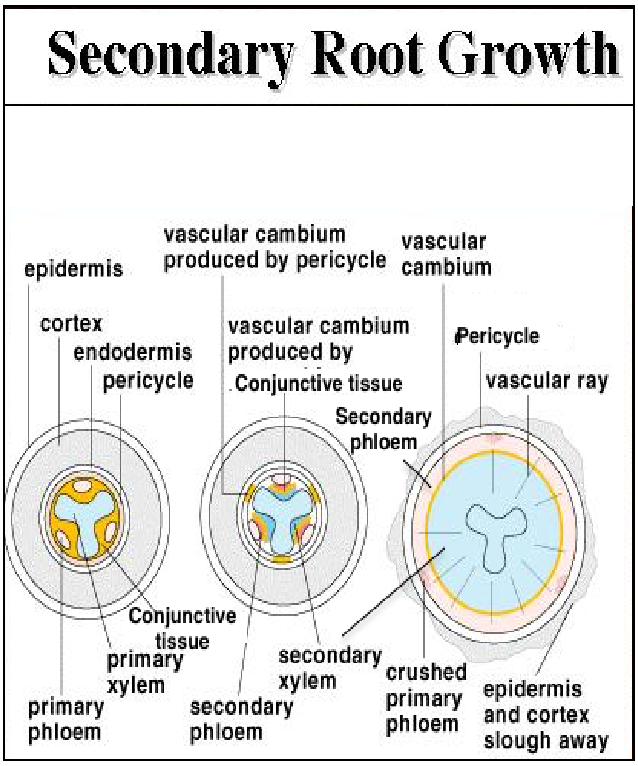
Heart Wood and Sap Wood

As the growth of the vascular tissue continues, the inner earlier formed xylem elements become nonfunctional and stop conducting water. The parenchyma cells die. This part of the wood then accumulates organic compounds such as tannins, resins, gums, oils, phenols, aromatic substances and essential oils that give it a dark colour and often fragrance. This wood is called the **heart wood**. The presence of these compounds makes the heart wood heavier, more durable and less susceptible to the attack of pathogens and insects.

The outer part of the wood containing living parenchyma cells is called the **sap wood**. A new layer of sapwood is formed each year. Functional xylem elements are present in this part of wood. It is more susceptible to the attack of pathogens and insects.

Secondary Vascular Growth in Root:

Roots possess vascular bundles which are radial and closed wherein xylem and phloem tissues alternate with each other and cambium is absent. A few layers of parenchyma cells, called conjunctive tissue lie between primary xylem and primary phloem.



Initiation of secondary growth occurs with the differentiation of conjunctive tissue into vascular cambium. The cells of conjunctive tissue become meristematic and form arcs of vascular cambium. These cambial cells divide and form secondary vascular tissue predominantly below primary phloem; secondary xylem tissue forms toward the inner (primary xylem) side while secondary phloem is produced on the outer side toward the primary phloem. Accumulation of secondary xylem on the inside pushes the cambial layer toward outside which eventually reaches to the outer end of xylem elements (tip of xylem arms/ridges). At this stage, the pericycle cells adjacent to the protoxylem become meristematic and join the arcs of cambial cells forming a complete cylinder of vascular cambium. Complete cylinders of secondary xylem inside and secondary phloem outside form through activity of the cambium. Commonly, the secondary xylem and phloem tissues formed in root are similar to those in stem except that much less secondary tissue forms in the former. Roots too, exhibit annual growth rings. The study of the secondary xylem of roots of perennial herbaceous plants in which the stems and leaves die after every growing season is known as "herb chronology".

As in the stem, in root too, more amount of secondary xylem as compared to secondary phloem is produced.

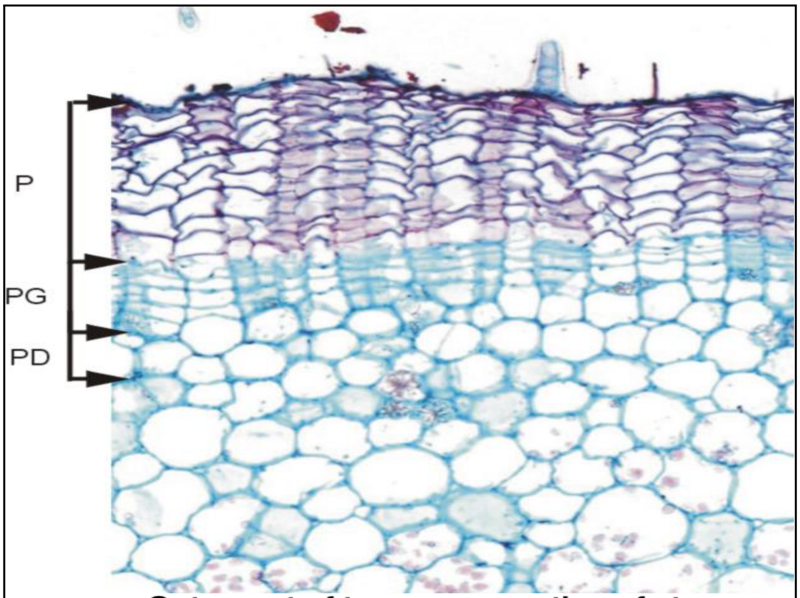
Formation of Periderm

Continuous accumulation of secondary vascular tissue increases the girth of stem and root. This increase in girth results in increased outer circumference. The cells at the periphery, including those of the outer secondary and primary phloem, pericycle, endodermis, cortex and epidermis, initially get stretched but later break with the expanding circumference. Rarely in some plants (without bark), these cells divide to keep pace with the increase in circumference. The broken outer parts are replaced by new tissues formed by another type of lateral meristem, the **cork cambium** or **phellogen.**

Phellogen or cork cambium develops in stems and roots of most dicots and a few monocots. It arises in the cortex or phloem tissue in stems, and from pericycle in roots. It cuts off cells on both sides. Cells formed on the outer side differentiate into cork cells (**phellem** cells) and cells cut off on the inner side form the **secondary cortex** or **phelloderm**. Phellogen is usually short-lived, lasting for only a few weeks. It then becomes cork and dies. Later a new cork cambium forms in younger tissues, in the secondary cortex or secondary phloem, and the cycle starts again. Over time many layers of cork can build up.

The cork or phellem consists of generally dead cells with primary cell walls encrusted with suberin making them impermeable to water and gases. The phellem is so impermeable that all tissues external to it (epidermis, cortex, older secondary phloem) die of lack of water.

The secondary cortex or phelloderm cells are living cells. In many plants the cork cambium produces very little (1-2 cell layers) or negligible amounts of phelloderm.



Outer part of transversesection of stem
P- Phellem, PG- Phellogen, PD- Phelloderm

The phellem, phellogen and phelloderm together are known as **periderm.** Because of continued growth in girth, periderm offers only temporary protection. It gets stretched, broken and sloughed off periodically. Fresh phellogen arises in the layers inner to the old phellogen and forms new periderm layers to provide protection.

Bark is a non-technical term used to refer to all the tissues outside the vascular cambium. It consists of secondary and primary phloem and all the layers of epidermis formed. Bark can be **soft** when it does not contain fibres (phloem), sclereids or other hard-walled cells and has sieve tubes with larger diameter and thinner walls. **Hard bark** contains sclerenchymatous cells such as fibres and sclereids, and sieve tubes with narrower lumen and thicker walls. Generally bark formed early in the growing season is soft and is referred to as **early bark** whereas bark formed toward the end of growing season is comparatively hard and is called **late bark**. Very often bark is distinguished into the **inner bark** containing mostly the living and functional tissues, viz. phloem tissue, phelloderm and the phellogen, and **outer bark**, technically known as **rhytidome**, consisting of dead cells exterior to the most recently formed phellogen.

The outer covering of cork cells with suberin encrusted walls prevents exchange of gases required for the survival and metabolism of inner living cells. To facilitate gas exchange, lenticels are formed.

Source: https://commons.wikimedia.org/wiki/File:Lenticels-sambucus_nigra.jpg

Lenticels are elongated, circular or oval openings in the bark and are made up of cells with large intercellular spaces. The cells, forming the **complementary tissue or filling tissue**, are produced by a meristem which is in continuation with the phellogen. The parenchyma cells may later develop suberized walls, lose their protoplasts and die. The intercellular spaces of the lenticels are continuous with those of the inner living cortical and phloem cells enabling gas exchange.

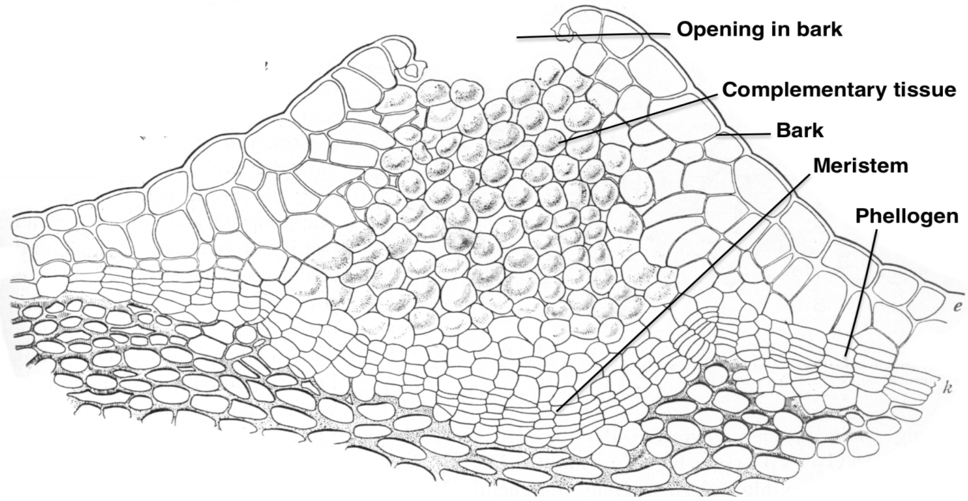


Diagram of Section of a Lenticel

Source: https://de.wikipedia.org/wiki/Lentizelle

Summary

Lateral meristems are responsible for the increase in girth of a stem or root of generally dicotyledonous plants. There are two types of lateral meristems, the vascular cambium and the cork cambium or phellogen. Vascular cambium produces secondary vascular tissues. It cuts off cells toward inside which form secondary xylem and cells toward outside that differentiate into secondary phloem. Fascicular and interfascicular cambium join to form the vascular cambium in the stem. In root, vascular cambium forms from the conjunctive tissue and pericycle. Annual rings found in wood are the result of seasonal variations in activity of vascular cambium.

Phellogen arises generally in the cortex in the stem and in the cortex or phloem in the root. Its activity produces a secondary cortex or phelloderm on the inner side and cork or phellem on the outside. Phellem, phellogen and phelloderm are collectively called periderm. Periderm forms the protective covering when the outer layers break and get sloughed off due to increasing diameter of the organ. Bark is a technical term given to all the tissues outside vascular cambium. Lenticels are openings formed in the bark to facilitate gas exchange between the inner living cells and outer atmosphere.