Course: B.Sc. Botany
Semester: III
Paper Code: BOT CC305
Paper Name: Anatomy of angiosperms
Topic: Normal secondary growth; Anomalous secondary growth in *Tinospora, Bignonia, Boerhaavia* and *Dracaena*
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Normal secondary growth

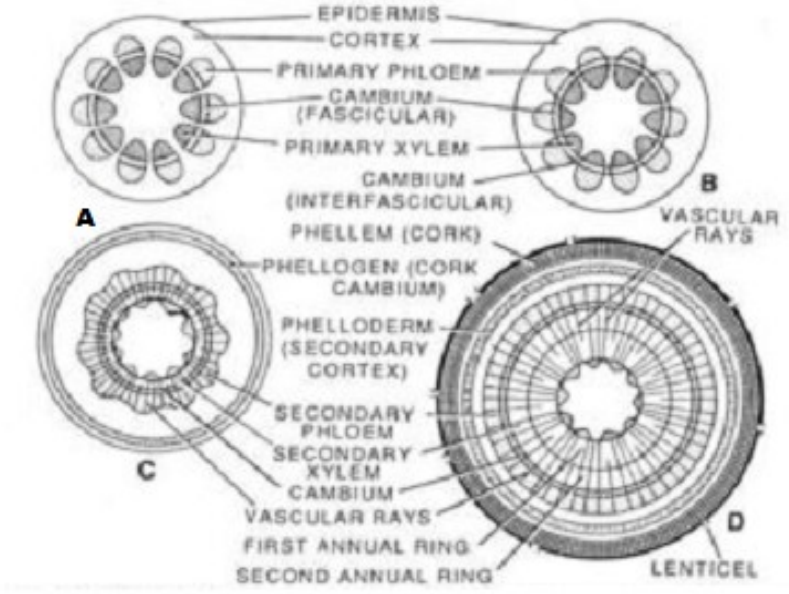
The increase in length of the shoot and the root is referred to as **primary growth**. It is the result of cell division in the shoot **apical meristem**. Sometimes, as in pteridophytes and monocots, the primary plant body is complete in itself and does not grow in thickness by the activity of lateral meristem.

However, in dicots, the primary permanent tissues make the fundamental parts of the plant and further growth in thickness is completed by cambial activity, called as **secondary growth.** Secondary growth is characterized by an increase in thickness or girth of the plant. It is caused by cell division in the **lateral meristem**.

The tissues formed during secondary growth are called as **secondary tissues.** Secondary tissues are of two types-

1. The **vascular tissues** (xylem and phloem) developed by the **vascular cambium**
2. The **protective tissues** (periderm) comprising of **cork** (phellem) and **phelloderm** (secondary cortex) developed by the **cork cambium** (phellogen).

Stages of secondary growth in a typical dicot stem



Secondary growth in thickness
A-D diagrams showing stages in secondary growth of a dicot stem

Stage A

- Vascular bundles of dicot stems are conjoint (xylem and phloem in one bundle), collateral (laterally placed on the same radius) and open (fascicular cambium present between xylem and pholem), arranged in a ring.

- Single layer of fascicular cambium is present between primary xylem and primary phloem. There is no cambium across the pith rays/ medullary rays.

Stage B

- After differentiation of xylem and phloem, the paranchymatous cells of pith rays between the edges of fascicular cambium become meristematic and connect to the fascicular (vascular) cambium. Thus, a complete ring of cambium (**intra**-fascicular cambium and **inter**-fascicular cambium) is formed.

Stage C

- The cells of the cambial ring divide continuously forming secondary xylem towards the inner side and secondary phloem towards the outside of the cambium ring, respectively. Thus, the vascular bundles increase in size.
- More xylem cells are formed towards the inner side as compared to phloem cells towards the outside.
- The inter-fascicular cambium cuts off paranchymatous cells on both sides forming the pith rays/ medullary rays, thus, pith rays also grow in length.
- The secondary xylem of the tree trunk is of great economical value, since it constitutes the timber and wood of commerce.

Stage D

- Due to continued formation of secondary tissues in the older stems, a pressure is exerted on the epidermis which ultimately results in the rupture of the epidermis followed by the death of epidermal cells and the cells below them.
- So simultaneously a protective periderm is formed in the epidermal, sub-epidermal, cortical or extra-stelar region depending upon different types of the plant. Formation of periderm is a common phenomenon during secondary growth as a protective measure for the internal tissues.
- Structurally, the periderm consists of three parts-
  (1) meristematic **phellogen** or **cork cambium**
  (2) the layer of the cells cut off by the phellogen on the outer side, the **phellem** or **cork**
  (3) the layer of the cells cut off by the phellogen on the inner side, the **phelloderm** or **secondary cortex**
- Usually in the periderm, **lenticels** originate beneath the stomata, comprising of loosely arranged **complementary cells** and help in exchange of gases between the atmosphere and internal tissues of the plant.

Anomalous secondary growth

The term 'anomalous' means abnormal. **Anomalous secondary growth** is an abnormal type of secondary growth. It is the result of deviation in the cambial activity from the normal type found in most of the dicots.

Important features of normal secondary growth-

- Secondary growth in plants is due to the cambial activity.
- Cambium is the lateral meristem normally present in vascular region.
- In dicotyledonous stems union of fascicular and inter fascicular cambium results into the formation of cambium ring.
- Cambium ring produces more xylem towards inner side and less amount of phloem towards outer side.

Any deviation or change in the normal secondary growth is referred as '**Anomalous or Abnormal secondary growth'.**

If anomalous secondary growth has relation with the habit or physiological function, such anomalous secondary growth is called **Adaptive anomalous secondary growth.**
If anomalous secondary growth has no relation with the habit or physiological function, such anomalous secondary growth is called **Non Adaptive anomalous secondary growth.**

The abnormal secondary growth can be studied under the following headings on the basis of cambial activity and distribution of secondary tissues-

I. Abnormal functioning of cambium
II. Unusual position of cambium
III. Formation of accessory cambial rings
IV. Formation of interxylary phloem
V. Secondary growth in monocotyldons

(I) Abnormal functioning of cambium

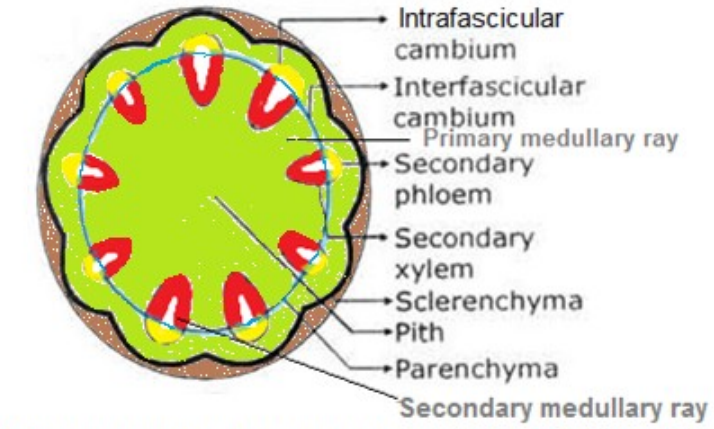
In this type, the cambium is normal in position but abnormal in activity. This type of anomaly is generally found in woody climbers (lianas) and the main purpose of abnormal behavior of cambium is to produce less xylem which is thick walled so as to make the plant more flexible to climb to its support without breaking. So it is **adaptive type of anomalous secondary growth.**

Cambia of this category functions in the following ways-

(a) In some cases, the inter-fascicular cambium forms non-vascular tissues and the vascular tissue formation is restricted to intra-fascicular cambium only (eg. *Tinospora, Aristolochia* etc.). At some spots, even the intra-fascicular cambium produces paranchymatous cells instead of vascular tissues resulting in fissured xylem.

Formation of fissured xylem as seen in ***Tinospora*** stem

- In many woody climbers or lianas like the stems of ***Tinospora*** (Family-Menispermaceae), the cambium produces the vascular tissues i.e. xylem and phloem only in the intra-fascicular region whereas in the inter-fascicular region paranchymatouc tissues are produced. Thus, the vascular bundles remain discrete, separated by paranchymatous tissues.
- In addition, even the intra-fascicular cambium at certain spots produces paranchymatous secondary medullary rays both towards the inside and outside instead of producing secondary xylem towards the inside and secondary phloem towards the outside.
- In this way, vascular bundles increase individually and become fluted 'V' shaped. Thus in the old stems, the xylem becomes fissured due to development of paranchymatous secondary medullary ray.
- The more of paranchymatous tissues and less of thick walled xylem tissue in the intra-fascicular and inter-fascicular regions make the plant more flexible and enable it to resist the pulling and compression due to the pressure of high wind.
- Also, when the stem grows around the support, the soft paranchymatous tissues prevent it from breaking or cracking.
- *Tinospora* is a woody climber, this anomaly is thus an adaptation to the climbing habit of the plant. Hence this anomalous secondary growth in *Tinospora* stem is described as **Adaptive anomalous secondary growth.**



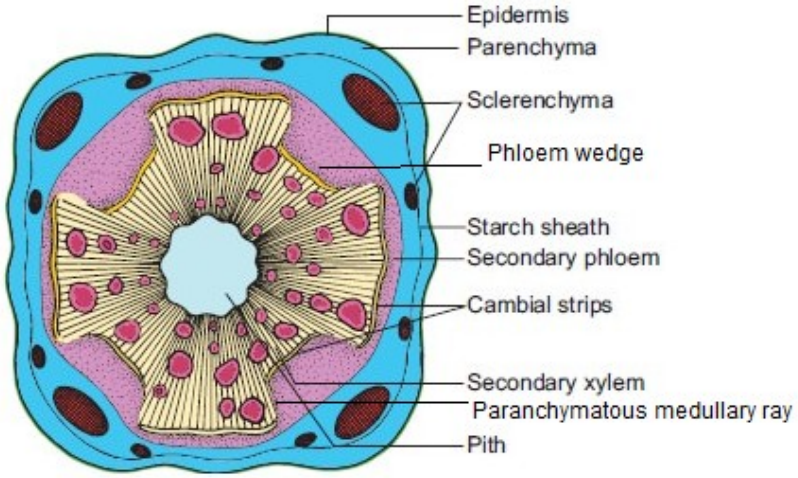
Anomalous secondary growth in *Tinospora* stem (diagrammatic)

(b) In some cases, the cambium produces more secondary phloem at certain spots as compared to secondary xylem forming phloem wedge embedded in xylem region (eg. *Bignonia*)

Formation of phloem wedge as seen in ***Bignonia*** stem

- *Bignonia* is a dicot woody climber belongs to family Bignoniaceae.
- Anomalous secondary growth in this stem is due to abnormal behaviour of normal cambium.
- The origin, position and function of cambium ring is normal in the initial stages of growth producing large amount of secondary xylem towards inner side and small amount of secondary phloem towards outer side.

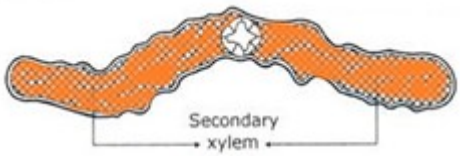
- In later stages of secondary growth, at several places (usually at four places in crosswise planes) the cambium starts cutting off more amount of secondary phloem towards the outer side and less amount of secondary xylem towards the inner side. This is abnormal behavior of cambium.
- These phloem patches later on get embedded or intruded deeply into the secondary xylem.
- This results in the formation of four deep wedges of secondary phloem in the secondary xylem region and a ridged and furrowed xylem cylinder is produced.
- The phloem patch is traversed by sclerenchyma bars which gives mechanical support to thin walled phloem tissues.
- The cambium is situated on the inside of the furrows and on the outside of the ridges, while the radial surface is occupied by paranchymatous medullary ray tissues.
- *Bignonia* is a woody climber, this anomaly is thus an adaptation to the climbing habit of the plant. Hence this anomalous secondary growth in *Bignonia* stem is described as Adaptive anomalous secondary growth.



Anomalous secondary growth in *Bignonia* stem (diagrammatic)

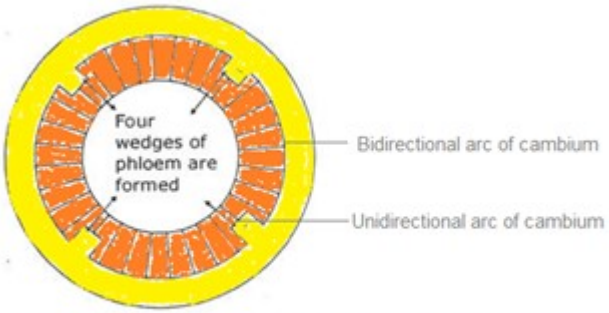
(c) In some other cases, the cambium activity is restricted to certain segments only where it cuts off cells actively while at other segments it is almost inactive or show limited activity, resulting in the formation of ridged stem (eg. *Bauhinia rubiginosa*). In *Bauhinia blumenaviana*, the cambial activity is restricted at two opposite side only and consequently a flattened strap like stem is produced.

Lobed stem of *Bauhinia rubiginosa* (diagrammatic)



Flattened stem of *Bauhinia blumenaviana* (diagrammatic)

(d) In yet some other cases like in the stem of *Doxantha*, furrow of secondary phloem are present in the cylinder of secondary xylem. It is due to the development of unidirectional and bidirectional arcs of cambium. Unidirectional arc of cambium produces little or no secondary xylem but extensive amount of secondary phloem, whereas the bidirectional arc of cambium produces as much or more secondary xylem than secondary phloem. Subsequently, four or more furrows of phloem are formed which act as shock absorber. Less of thick walled xylem tissues and more of thin walled phloem tissues allow the stem of this woody climber to bend during strong winds. A solid xylem core may not provide such flexibility..



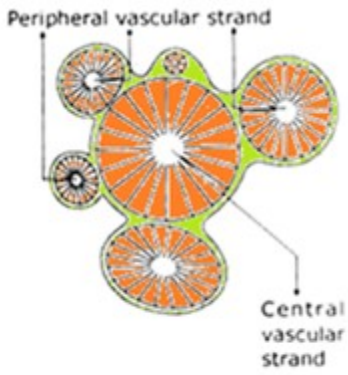
Anomalous secondary growth in *Doxantha* stem (diagrammatic)

(II) Unusual position of cambium

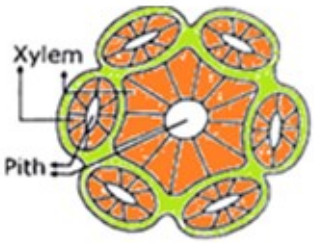
In this type, the position of cambium is unusual resulting in the formation of anomalous structure during secondary growth. This type of anomaly is found in *Thinouia, Serjania* etc.

Corded xylem mass in ***Thinouia*** stem

- In the young stem of *Thinouia*, belonging to the family Sapindaceae, the cambium is thrown into folds instead of a circular ring.
- As secondary growth proceeds, the cambium at folds become constricted and separated.
- After separation, each fold of cambium develops into a stele. The cambium cuts off secondary xylem towards the inside and secondary phloem towards the outside enclosing a pith.
- The production of such peripheral steles around the central stele gives a peculiar shape to the stem



Anomalous secondarry growth in *Thinouia* stem (diagrammatic)

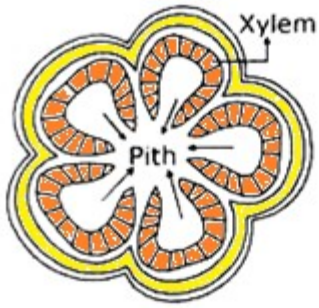


Corded xylem mass

Anomalous secondary growth in *Thinoia ventricosa* (diagrammatic)

Divided xylem mass in ***Serjania*** stem

- In some tendril climbers like *Serjania corrugate*, belonging to the family Sapindaceae, certain groups of vascular bundles become separated from the cylinder of primary vascular bundles.
- As the secondary growth proceeds, each strip of cambium forms a separate cambial ring that functions normally producing secondary xylem towards the inside and secondary phloem towards the outside.
- Initially the peripheral pith is continuous with the central pith but later on they separate.
- Thus the stem comprises of several discrete vascular cylinders each of which ultimately develops its own periderm and the stem appears to be made up of several fused stems.



Divided xylem mass
Peripheral vascular bundle
in *Serjania corrugata* (diagrammatic)

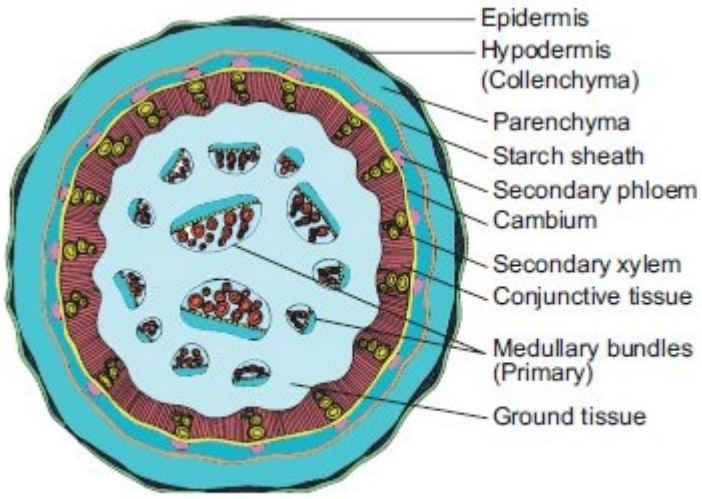
(III) Formation of accessory cambial rings

Usually one cambial ring is responsible for the secondary growth in dicots throughout the life. But in some plants like *Boerhaavia, Bougainvillea, Achyranthus* etc., more than one accessory cambial rings are formed during secondary growth which is an anomaly. It is non-**adaptive type of anomalous secondary growth.**

Formation of accessory cambial ring in ***Boerhaavia*** stem

- *Boerhaavia* belongs to the family Nyctaginaceae and shows non-adaptive type of anomalous secondary growth.
- The stem of *Boerhaavia* shows both primary anomaly as well as secondary anomaly.
- The primary anomaly is the presence of three rings of vascular bundles instead of the normal one ring. There are two largest innermost medullary vascular bundles encircled by second ring of 6-14 middle sized medullary vascular bundles followed by numerous small outermost ring of vascular bundles.
- During secondary growth, no cambial ring is formed in the central most and middle ring of medullary vascular bundles.
- The cambial ring is formed in the outermost ring of vascular bundles. The intra-fascicular cambium cuts off secondary xylem towards the inside and secondary phloem towards

- the outside while the inter-fascicular cambium suts off thick walled conjunctive tissues on both sides.
- After sometimes, the cambium ceases to function and a new cambium is formed outside the first cambium.
- The process is repeated at intervals for four or more times.



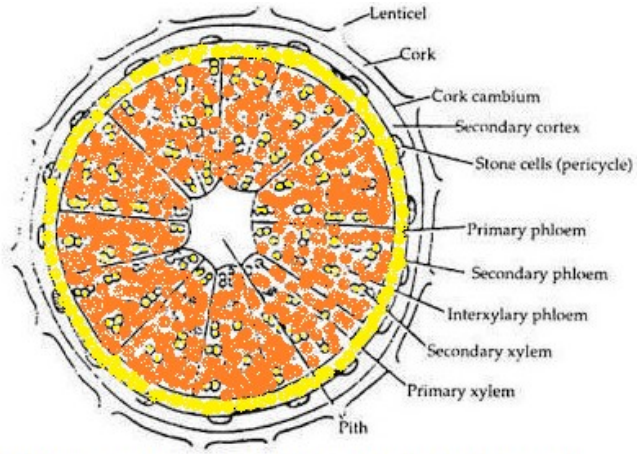
Anomalous secondary growth in *Boerhaavia* stem (diagrammatic)

(IV) Formation of interxylary phloem

In this type of anomaly, interxylary or included phloem develop by variation in cambial activity during secondary growth and they remain surrounded by secondary xylem. This type of anomaly is found in plants like *Salvadora, Combretum* etc. It is **non-adaptive type of anomalous secondary growth.**

Formation of interxylary phloem in ***Salvadora*** stem

- *Salvadora* belongs to the family Salvadoraceae.
- In this case, during secondary growth, small segments of cambium produce secondary phloem towards the inside instead of secondary xylem.
- This abnormal activity of cambium continues for some time and then stops.
- Later, the normal activity of cambium is restored by production of secondary xylem towards the inner side.
- As a result, the secondary phloem formed towards the inner side for a short period gets embedded in the secondary xylem elements.
- These groups of embedded phloem are called as ‘interxylary phloen’ or ‘pholem islands’ or ‘included phloem’.



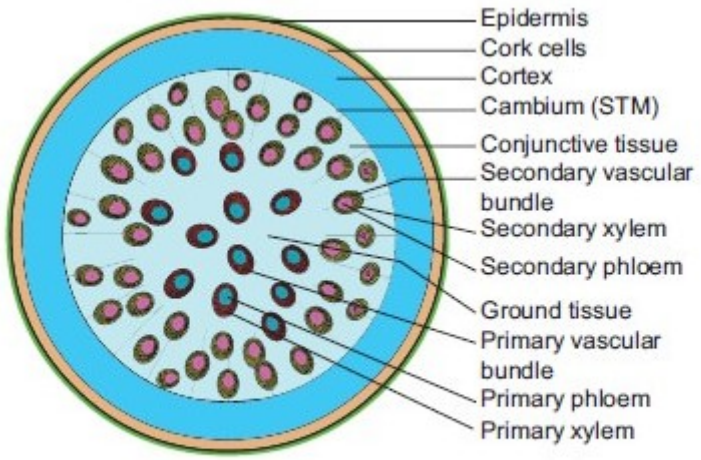
Anomalous secondary growth in *Salvadora* stem (diagrammatic)

(V) Anomalous secondary growth in monocotyledons

The vascular bundles of monocotyledons are closed, i.e. cambium is absent. So, usually secondary growth does not take place in mocotyledons, but there are some exceptions like *Dracaena*, *Aloe, Agave* etc. So secondary growth in monocots is in itself an anomaly.

Secondary growth in ***Dracaena*** stem

- *Dracaena* belongs to the family Agavaceae.
- As *Dracaena* is a monocot, the vascular bundles are scattered in the ground tissue. The cambium appears in the parenchyma outside the outermost vascular bundles.
- The newly formed cambium cuts off towards outside and inside both.
- The tissues developed on the inner side of the cambium, becomes differentiated into concentric vascular bundles.
- The cells formed on the outer side of the cambium forms parenchyma.



Anomalous secondary growth in *Dracaena* stem (diagrammatic)