Vascular Cambium: Origin and Activities

Origin of Vascular Cambium:

- In stems the vascular cambium and the primary vascular tissues differentiate from procambium. Procambium develops from the derivative cells of apical meristem. Transverse sections of a growing vegetative shoot apex reveal the presence of a cylinder of cells that are highly cytoplasmic and more densely staining. This ring of cells is regarded as a residuum of the meristematic tissue of apical meristem and so termed as residual meristem. Within the residual meristem more densely staining regions are present and these regions have a topographic relationship with leaf primordia. This region constitutes procambium that develops as leaf trace.
- The remainder of residual meristem forms the interfascicular parenchyma. In longitudinal section of vegetative apical shoot of angiosperm and gymnosperm it is observed that the procambial ring or strand is continuous and develops acropetally (Figs. 23.2 & 23.3).
- Procambial strands exhibit two waves of differentiation, that is, differentiation of protophloem on the peripheral side and differentiation of protoxylem towards the inner edges in normal angiosperm.

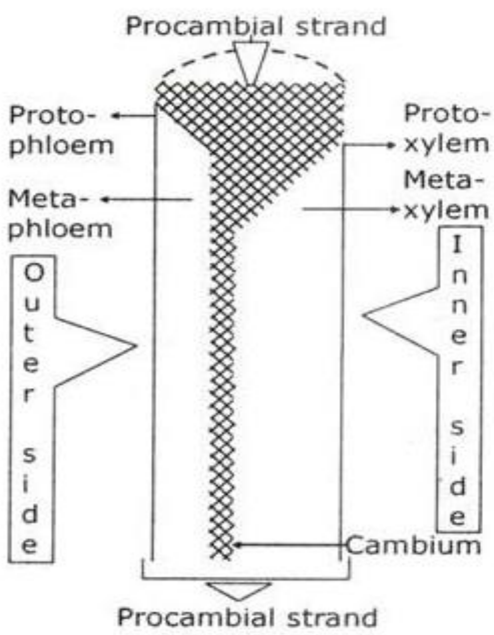

Figure 23.2

Schematic diagram of longisection of procambial strand from the apex to illustrate the mode of origin and development of xylem and phloem. Proto-phloem originates earlier than proto-xylem. The edges of procambium strand differentiates before than centre. The undifferentated region of procambium becomes cambium

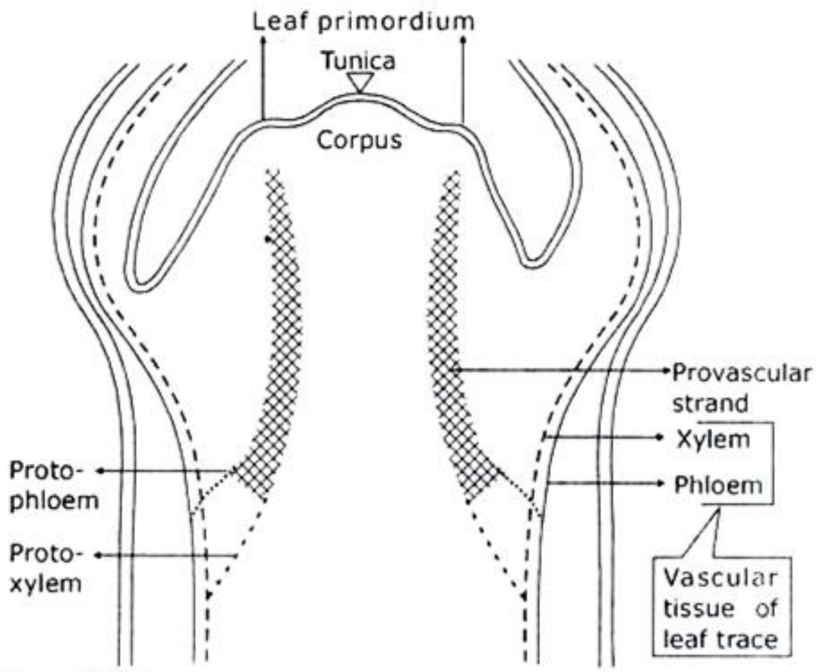

Figure 23.3

Diagram of longisection of angiosperm shoot apex illustrating the topographical relationship between leaf primordium and provascular strand, and representing the linkage of differentiating provascular strand and existing leaf trace.

- ``In monocotyledons the two waves of differentiation meet and the whole procambial strand form the primary vascular tissue. In most dicotyledons these waves do not meet. A zone of procambial meristematic cells remains. This zone that occurs between primary xylem and-phloem is the vascular cambium. If it is not in the form of a continuous ring, a continuous ring of cambium is formed by dedifferentiation of interfascicular parenchyma into interfascicular cambium and their subsequent lateral union with fascicular cambium.
- ``Procambium gives rise to permanent tissues and it is customary to designate the tissues as primary. The derivative cells of cambium are designated as secondary. In normal dicotyledonous stem the ring of vascular cambium is composed of fascicular and interfascicular cambium.
- In the normal dicotyledonous root the vascular cambium is wavy. There is no distinction between fascicular and interfascicular cambium. The ridges of the wavy cambium occur overarching the protoxylem while the furrows lie below the primary phloem.

Activity of Vascular Cambium:

- The vascular cambium is one cell thick and the cells of cambium are compactly set without having any intercellular spaces. Cambium and its immature derivatives form a cambial zone where it is difficult to differentiate the cambial initial. Two types of mitotic divisions characterize an active cambium-periclinal and anticlinal. As a result of periclinal divisions new cells of secondary xylem and-phloem are produced. Anticlinal divisions give rise to new cambial initials.
- At the time of secondary growth the fusiform initial divides periclinally. One of the two cells thus formed remains as fusiform cambial initial whereas the other is an immature cambial derivative that is added to the cambial zone (Fig. 23.4). The fusiform cambial initial continually cuts of new cambial derivatives to the exterior and to the interior.

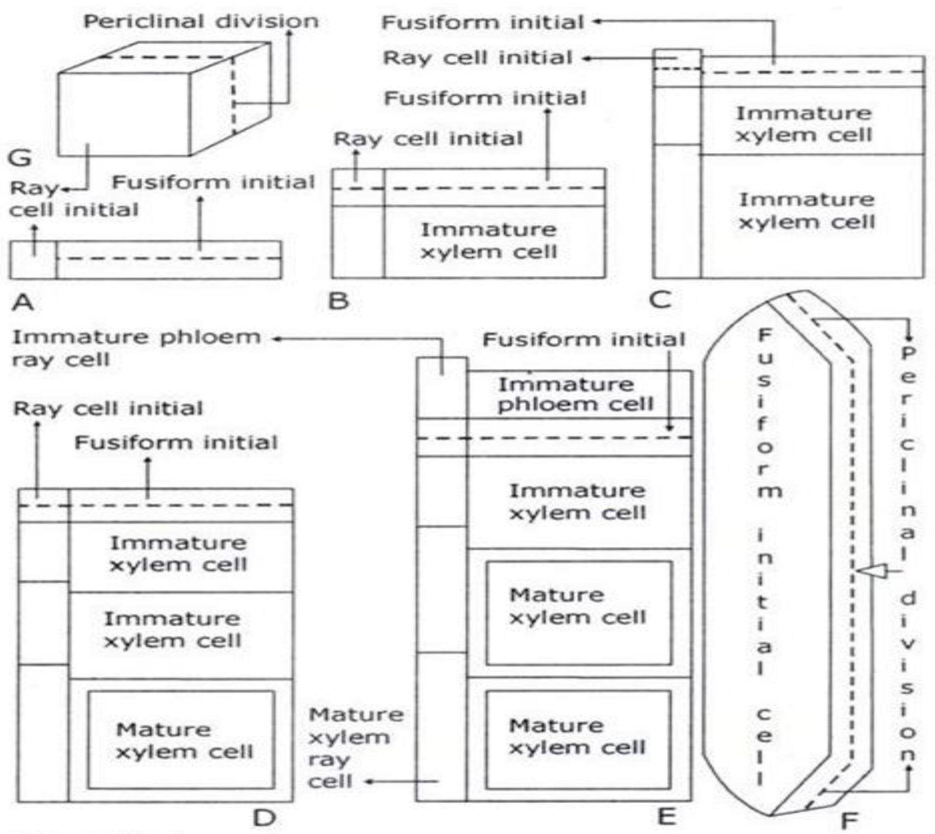

Figure 23.4

Schematic drawings of the production of secondary xylem and secondary phloem by cambial initial cells (A-E).
Broken lines indicate periclinal division.
F. & G. are fusiform initial and ray cell initial in three dimensional view respectively

- The derivative cells may differentiate directly into new secondary phloem to the exterior and new secondary xylem to the interior. In this case the cambial zone is narrow. But more commonly the cambial initial and its derivative cells divide further. As a result a wide cambial zone is formed. Continued periclinal divisions in fusiform cambial initials and in their derivative cells result in radially oriented files of cells of similar shape that mature to secondary vascular tissues. Such radial oriented files of cells are conspicuous in the secondary xylem of conifers where the secondary xylem is largely composed of tracheids.
- In angiosperms (Fig. 23.5) such radial files of cells are less conspicuous due the formation of vessels. Vessels often increase greatly in diameter and as a result distortion of files occurs. As the fusiform initials compose the axial system of vascular cambium, their derivatives mature into the elements of vascular tissues that compose the axial system. The derivative cells mature into tracheids, trachea and xylem fibre of xylem and sieve tube, companion cell and phloem fibre of phloem as they compose the axial system of plants.

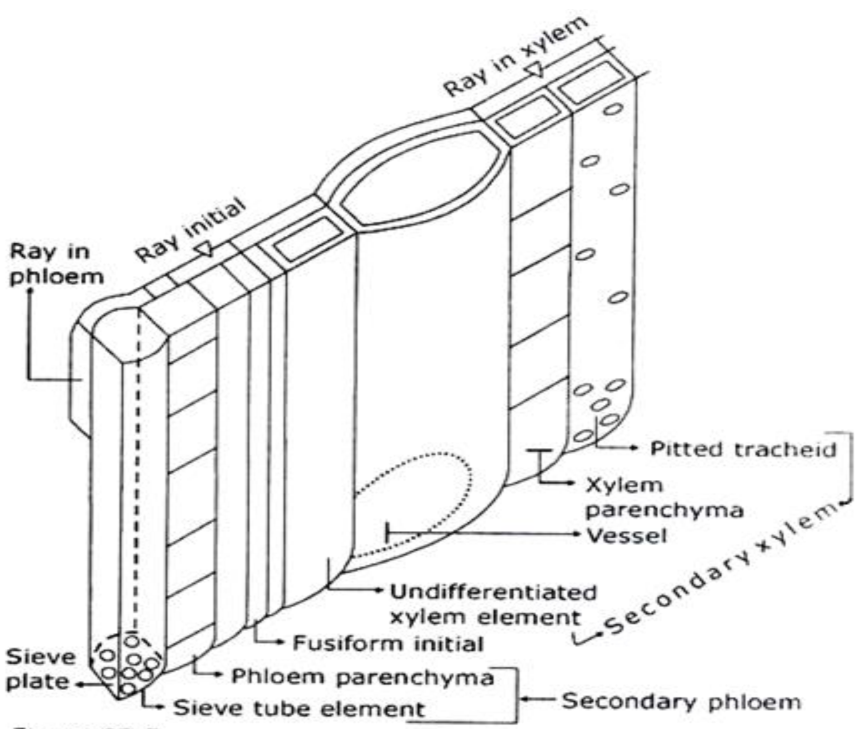

Figure 23.5

A diagrammatic interpretation of the production of secondary vascular tissues by cambium

- The ray cell initial divides periclinally to form two cells. One of the daughter cells remains as cambial ray initial. The other cell differentiates into either xylem parenchyma if it is the inner cell or phloem parenchyma if it is the outer cell. Ray initials produce mostly xylem and phloem parenchyma.
- In gymnosperm ray initials form albuminous cell. The ray initial and its derivatives compose the radial system of plants. In a cambial zone only one layer of true cambial initials is present. Periclinal division in a cambial cell forms two cells. One of the daughter cells differentiates into secondary xylem or —phloem. The other cell retains its meristematic properties. This process continues throughout the life of a plant and therefore the division of cambium is limitless. This virtual immortality of cambial cells ideally displays the 'continuing meristematic residue' of Newman (1965). The derivatives of cambial initials are incipient vascular tissues. They differentiate into secondary xylem cells and secondary phloem cells. Normally the amount of secondary xylem formed is in excess in comparison to secondary phloem.
- The ratio of differentiation between secondary xylem and secondary phloem is 3 to 1 in conifers.
- In dicotyledons the ratio is variable and may be as great as 10 to 1. In an experiment *Eucalyptus camaldulensis* was exposed to labeled $^{14}CO_2$ that was incorporated in secondary vascular tissues. The incorporation of $^{14}CO_2$ indicates that the ratio of layers of secondary xylem and — phloem produced by the cambium is 4 to 1.
- The cambial activity is related to rainfall and temperature in tropical and temperate zone respectively. In tropical zones the vascular cambium of some species is continually active throughout the entire life. In temperate zones the vascular cambium remains dormant in winter. It activates in spring and produces secondary vascular tissue.
- Activation and cessation of cambial activity occur at an earlier age in ring porous trees (e.g. *Quercus*) than in diffuse porous trees (e.g. *Fagus*). There is experimental evidence that day-length affects the duration of cambial activity. In short-day condition the cambium remains dormant in *Robinia pseudacacia*.
- Activation/reactivation of cambial activity followed by a period of dormancy occurs over the entire life of a plant. It leads to the formation of growth rings that reveal approximate

age of plant. Thus the age of Pinus aristata and Sequoiadendron was estimated to be more than three thousand years.

- The cambial activity causes the increase in girth of axis. The circumference of vascular cambium also increases to cope up with the increase in girth of axis. This is accomplished by the formation of new fusiform- and ray initials.

Formation of the fusiform cambial initial occurs in the following ways:

- Fusiform initials in a storied cambium divide by anticlinal divisions and thus new initials are added to cambium.
- Short fusiform initials divide by radial anticlinal divisions where the partition walls occur parallel to long axes (Fig. 23.6A-C).
- The production of new initials from long non-storied fusiform initials occurs by oblique anticlinal divisions with walls of various degrees of inclination (pseudo-transverse). The daughter cells thus formed elongates by apical intrusive growth of overlapping ends.
- The elongation and intrusive growth of ray cell initials may form new fusiform initials. The elongation of ray cell initials occur parallel to the long axis of plants (Fig. 23.6D-E).

Fusiform initials give rise to ray initials in the following ways:

- An entire or part of short fusiform initial divides by a series of transverse anticlinal divisions thus forming a tier of ray cell initials (Fig. 23.6F).
- Fusiform initial cuts off a single cell on its lateral side by an arcuate wall. In the small lateral daughter cell series of transverse anticlinal division occur and as a result a new ray initial is formed (Fig. 23.6G).
- Fusiform initial cuts off a single cell at its end (Fig. 23.6H).
- A fusiform initial is reduced to a ray cell initial (Fig. 23.6I).

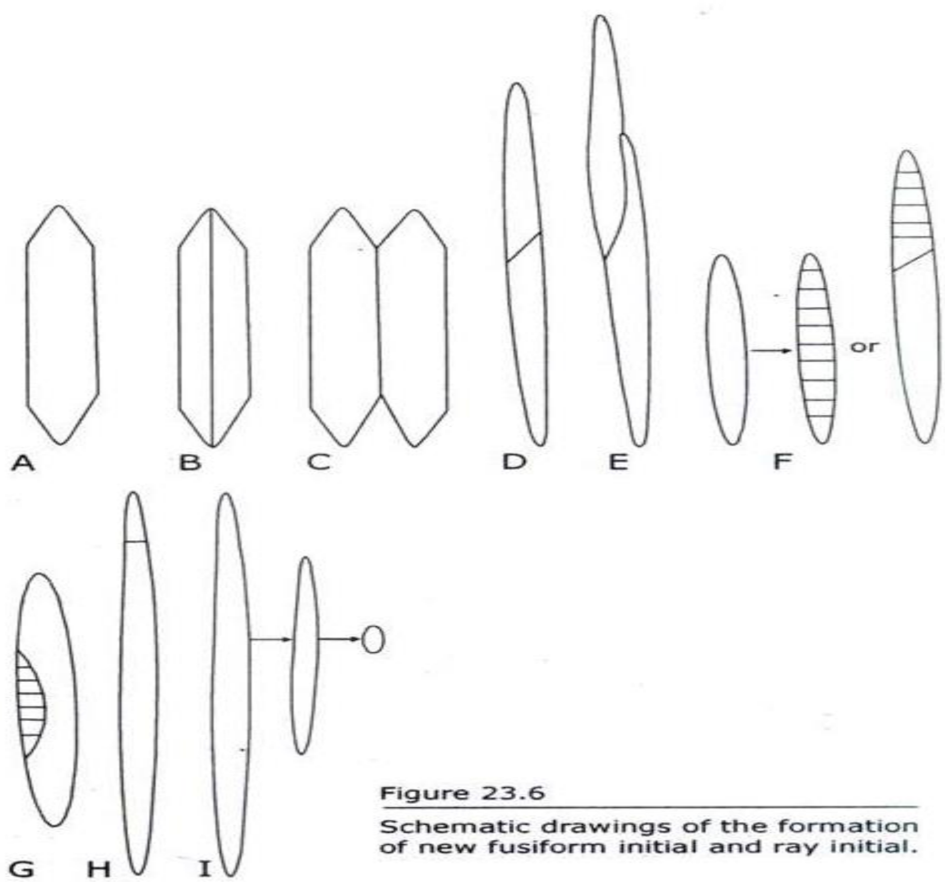

Figure 23.6

Schematic drawings of the formation of new fusiform initial and ray initial.

- In the above cases a uniseriate ray initial is formed. The ray initials may divide by a series of longitudinal anticlinal divisions to form biseriate or multiseriate rays.
- During secondary growth as the cambium increases in circumference a balance between the number and distribution of fusiform- and ray initial is always maintained, because rays are the passageways for the transport of nutrients to cambium and its immediate incipient derivatives.
- In case of dicotyledons the wavy cambium of root donates secondary xylem towards interior and secondary phloem towards exterior. The portion of the wavy cambium ring that occurs at the furrow forms more secondary xylem. As a result at later stage of development the wavy ring becomes more or less circular.
- In dicotyledonous stem the fascicular cambium becomes active before the differentiation of interfascicular cambium (Fig. 23.7A-D). In many plants at the interfascicular region there originate provascular strands.

- The strands arise close to the initial vascular bundles (Fig. 23.7B). At later stage differentiating provascular strands and initial vascular bundles may contact to each other laterally thus forming vascular cambium continuous across the vascular bundles (Fig. 23.7C & D).

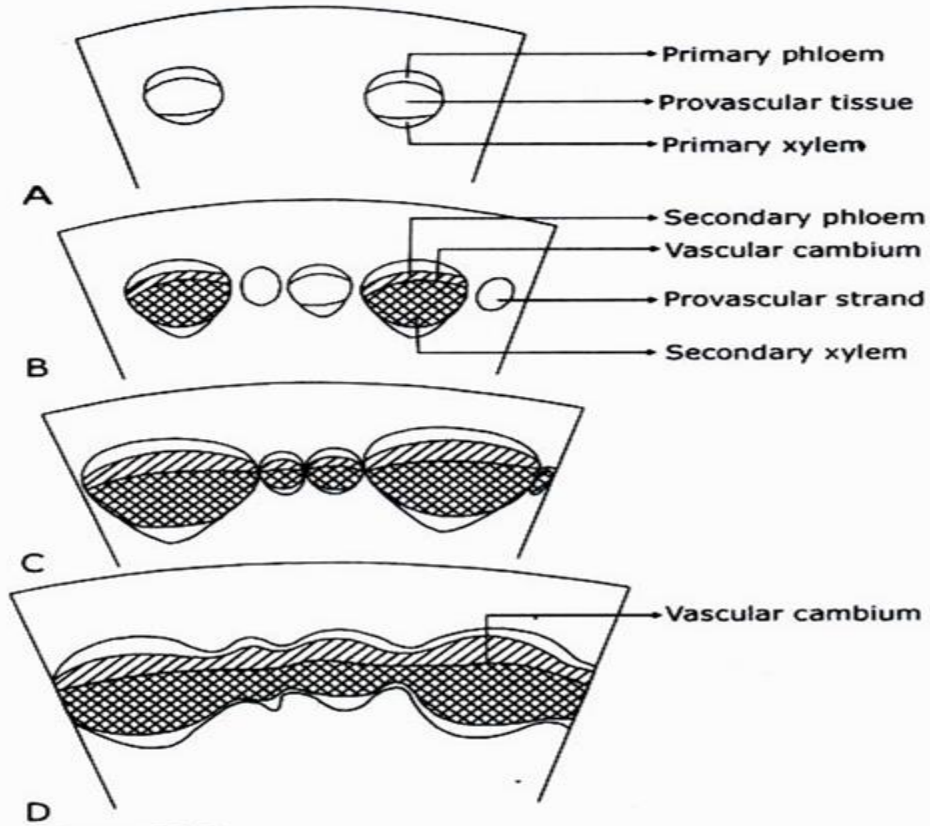

Figure 23.7

Diagram illustrating stages of formation of provascular strand, vascular cambium and secondary vascular tissues. Secondary xylem = crosshatched. Secondary phloem = obliquely hatched.

- In many woody herbs (Fig. 23.8A & B) interfascicular cambium originates from ground meristem when it differentiates early. In later stages mature interfascicular parenchyma by dedifferentiation forms interfascicular cambium.
- The fascicular cambium becomes active initially in the vascular bundles. When the vascular cambium becomes continuous and complete, the derivative cells of cambium cause the increments of secondary vascular tissues in normal secondary growth.
- In herbaceous dicotyledons, e.g. Geum, Agrimonia etc. (Fig. 23.8D) the fascicular cambium is active only. In Ranunculus, Impatiens etc. (Fig. 23.8E) cambium does not

develop usually or if it develops it remains inactive. In annuals the vascular cambium remains active only during the growth of the plant and ceases its activity before the plant dies. The vascular cambium functions throughout the life of woody perennials.

- It is to note that vascular cambium is absent from most monocotyledons, pteridophytes and some herbaceous dicotyledons. In woody lianas, e.g. Aristolochia, Clematis etc. (Fig. 23.8C) the derivatives of fascicular cambium differentiates into characteristic secondary xylem and- phloem. But the derivative cells of interfascicular cambium differentiate into parenchyma cells only. This type of cambial activity is regarded as abnormal.
- Anomaly in the activity of cambium is also observed in *Serjania, Paullinia*. Thinouia etc. where in stems the cambium ring is split into several isolated segments that form separate vascular strands, often in a regular pattern.
- In *Bauhinia* stem different sectors of cambium donate unequal amount of secondary xylem and as a result the stem becomes lobed. In Bignonia stem symmetrically located segments of cambium cease to form xylem inwards and form phloem in excess outwards. As a result xylem becomes separated by radial slits.

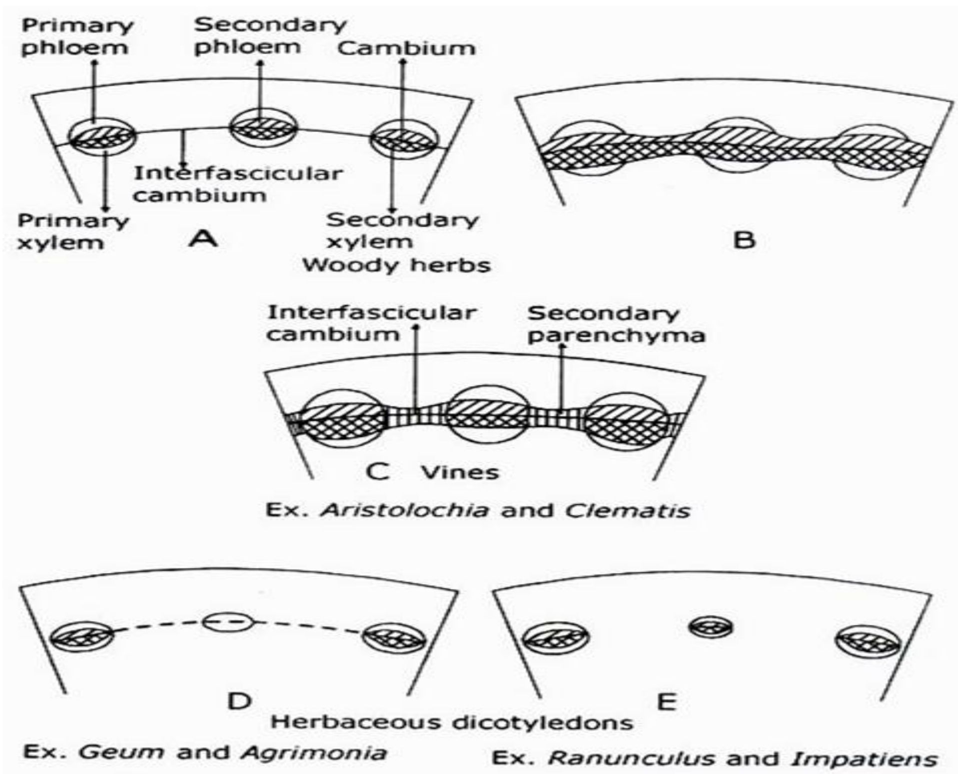

Figure 23.8

Diagram showing fascicular cambium, formation of interfascicular cambium, formation of secondary xylem (= crosshatched) and secondary phloem (= obliquely hatched).

Accessory cambium:

- Accessory cambium develops both in stems and root. In the stem of Amaranthus, Boerhaavia, Mirabilis etc. this secondary cambium originates on the peripheral side surrounding vascular bundles. Accessory cambium divides and the derivative cells differentiate into conjunctive tissue and secondary vascular bundles. In Tecoma stem two arcs of accessory cambium develop at the peripheral margins of pith.
- The cambium produces vascular tissues that have inverse orientation, i.e. secondary xylem on the peripheral side and secondary phloem (intraxylary phloem) on the inside. Accessory cambia also develop in monocotyledon (ex. Dracaena). In Dracaena accessory cambium forms thin-walled conjunctive tissue and leptocentric vascular bundles towards the inner side.
- In the root of *Beta vulgaris* concentric rings of accessory cambia originate in succession outwards. Most of the derivative cells store nutrients and as a result Beta root swells.
- Cheadle (1937) reported the existence of vascular cambium in monocotyledon. The cambium occurs at the peripheral region of the stem. The peripheral parenchyma divides to form the vascular cambium. The cambial cells are narrow and elongated, ex. Agave.
- The cells may be fusiform, polygonal or rectangular in shape. The cambium divides and the inner derivatives differentiate into vascular bundles, consisting of both xylem and phloem. The peripheral derivatives form parenchyma only. The vascular bundles, thus formed, remain embedded in the ground parenchyma.

Cork Cambium:

- Cork cambium, also known as phellogen, is a secondary lateral meristem. It originates from the permanent cells of epidermis, hypodermis, cortex and phloem by dedifferentiation.
- The cells of phellogen are compactly set without any intercellular spaces and rectangular or radially flattened in cross- sectional view. In longitudinal section they are rectangular or polygonal and sometimes irregular in outline. Each cell of phellogen is highly vacuolate and may contain chloroplast and tannins.
- The phellogen divides periclinally and the derivative cells differentiate into peripheral phellem (also called cork) and inner phelloderm. Cork cells have suberized cell walls that are impervious to air and water, and have protective properties. Phellem, phellogen and

phelloderm are collectively called periderm. Periderm forms a protective layer in stems and roots.

The following factors influence the cambial activity:

i. Hormone:

- It was first shown by Jost, 1893 that the activity of stem-cambium is greatest just below the growing leaves. In later years after the discovery and identification of indole-3-acetic acid (IAA) and after various experiments it was definitely concluded that the stimulus that activates the cambium is hormonal in nature.
- Hormone is produced in young buds and leaves and it is translocated downwards thus stimulating the cambium to divide. It was previously mentioned that the activity of cambium is highest in spring in the trees of temperate regions. It gradually declines as summer advances. In spring new buds develop where hormones are produced.
- Hormones move basipetally and then the growth activity of cambium is initiated and promoted. Later researches reveal that the interactions among IAA, gibberellic acid (GA) and 6-furfurylaminopurine (Kinetin) stimulate the division of cambium. In an experiment the shoots of Acer pseudoplatanus were completely disbudded. It was treated with IAA only and the formation of xylem was observed.
- It was noted that narrow zone of xylem was formed where the vessels were lignified only. The other disbudded shoots were treated with GA alone. In this case xylem was produced and they were non-lignified and without vessels.
- But a normal and wide zone of xylem was formed when the disbudded shoots were treated both with IAA and GA. This reveals that there exists a correlation between hormones in initiating the cambial activity.

ii. Gravity:

- In the branches of gymnosperm and angiosperm a special type of wood is formed termed reaction wood. In gymnosperm branches the reaction wood is formed on the lower side and is specially called compression wood. In the branches of angiosperm the reaction wood is formed on the upper side and is specially termed as tension wood. The reaction wood is the collective term of tension wood and compression wood.
- Various experiments reveal that these unequal proportions of wood are formed with respect to gravity. Gravity is the stimulus that causes the formation of reaction wood and

there are ample evidences that auxin is present behind the process. In an experiment plants were grown in klinostat and it was noted that no reaction wood is formed. This proves that reaction wood is formed in response to gravity.

iii. Day length:

- In short days late wood is formed only, e.g. Robinia. In this wood no vessels are formed. The vessels, if formed, are few in number and with small diameter. In long days early wood is formed. In this wood many vessels are developed and they have large diameter. In long days tracheids with large diameter are formed in conifers in contrast to short days where tracheids with narrow diameter are formed.
- In long days the needles of conifers elongate and there is no doubt that this is associated with auxin production. The production of auxin promotes to form tracheids with large diameter. In an experiment short day (i.e. long night) plants were given a low intensity of light for a short time during the long night period. It was observed that tracheids of wide diameter were formed.
- It indicates that the cambial activity is influenced by day length and it is a true photoperiodic phenomenon. Temperature influences the activity of cambium.
- It was observed that in Robinia seedling the activity of cambium was continuous for a long period when the plants were kept in a high temperature and short days. There exists a correlation between high summer temperature and cambial activity in the tropical tree Polyalthia longifolia.

iv. Pressure:

- The vascular cambium always remains compressed by the tissues present on internal and peripheral side of it. It is needed for the normal functioning of cambium. In an experiment with Pinus strobus and Populus trichocarpa the pressure was released on the peripheral side. Releasing a strip of bark from the tree by incisions while the apical end is still attached with the tree did this.
- Aseptic measures were taken and the operated zone was wrapped in polythene to prevent infection and reduce desiccation. After a few days it was noticed that an unorganized callus was formed on the inner side of the free strip of the bark and the function of cambium was not normal.

- In another experiment the pressure was released according to the previous experiment and then the pressure was applied by binding the strip of bark with the tree. Aseptic measures were taken as usual and after a few days it was noticed that no callus tissue was formed and the cambium functioned normally. This implies that pressure influences the normal cambial activity.
- The dominant features of vascular cambium are in its origin at a definite position in stems and roots, and production of xylem and phloem in relation to poles. The xylem is formed towards the inner side and the phloem is produced towards the peripheral side. This inherent polarity was demonstrated by Siebers (1971) in the following ingenious experiment with the hypocotyls of Ricinus communis (Fig. 23.9).

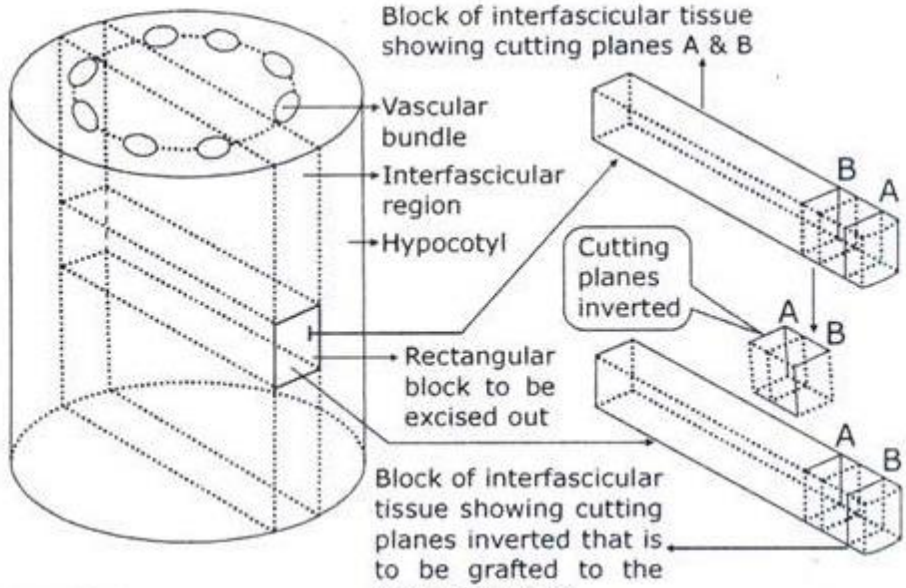

Figure 23.9

Diagram illustrating the experiment of Siebers on the hypocotyl of *Ricinus communis*.

- A rectangular block of tissue from the interfascicular region of hypocotyl, where the interfascicular cambium was supposed to originate after several days, was excised out. This tissue was grafted to the original position but with inverted cutting planes. Rotating the block of tissue with cutting planes through 180° did this.
- The successful grafts showed that xylem was produced on the peripheral side and phloem was formed towards the inner side. This proves that the production of vascular tissues by

the cambium is predetermined and the same tissues are formed in the same position even when the polarity of cambium is changed.

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