CHAPTER 7 Secondary Growth in Thickness

● **7.1 Definition and Occurrence :** A type of growth that occurs distant from the apices as a result of *increase in girth* or *thickness* of stem and root through the formation of *secondary* vascular and other tissues by the activities of lateral meristems like *vascular cambium* and *phellogen* (i.e. cork cambium) is referred to as *secondary growth in thickness.* The tissues thus produced during secondary growth are termed secondary tissues. These tissues constitute secondary body of the plant.

Secondary increase in thickness is noticed in gymnosperms, woody and some herbaceous dicotyledons, and also in some monocotyledons,—this type of growth starts as soon as the primary increase in thickness (due to the enlargement and divisions of the cells of primary tissues by the activities of apical meristems) stops.

● **7.2 Secondary growth in a typical dicotyledonous stem :** Typical *i.e.* common type of secondary growth is found in erect stems like those of members of Compositae, Tiliaceae, etc. and in many other dicots.

In stem, the secondary growth in thickness is confined both in the intrastelar (i.e. within the stele) and in the extrastelar (outside the stele, i.e. in the cortex) regions. The secondary growth of stem is brought about by the activity of the lateral meristem termed cambium (Fig. 7.1).

◆ **I. GROWTH IN INTRASTELAR REGION :**

(a) Formation of Cambium ring—**The cambium of the vascular bundle is called** ***fascicular cambium.*** Some of the living parenchyma cells of the medullary rays, mostly in a line with the fascicular cambium, become meristematic and form new strips of meristems known as *interfascicular cambium*—these two cambia i.e. fascicular and interfascicular cambia join with each other to form a complete i.e. continuous ring known as *cambium ring.*

(b) Formation of Secondary tissues—It is to be noted that in some cases, fascicular cambium of each vascular bundle at the onset of secondary growth gives off new secondary tissues on the outer and on the inner side. But in general, the cambium ring as a whole becomes actively meristematic and cuts off new cells both externally and internally. New cells cut off on the outerside of the cambium ring are gradually converted into phloem elements—these phloem elements constitute the *secondary phloem* which consists of sieve tubes, companion cells, phloem parenchyma and often also some patches of bast fibres.

Several important fibres of commerce e.g. jute, hemp, flax, ramie, etc. are the bast fibres of secondary phloem.

The cells cut off on the inner side of the cambium ring are gradually converted into different elements of xylem which constitute secondary xylem tissue—the *secondary xylem* consists of scalariform tracheae, tracheids, large amount of wood fibres usually arranged in radial rows and some wood parenchyma.

It is to be noted that the cambium is more active on the inner side than on the outer side of the ring—as a result, large amount of secondary xylem is formed than phloem which very soon forms a compact mass. Hence after secondary growth, secondary xylem forms the main bulk of the plant body. Owing to continuous formation of secondary xylem, a pressure is exerted by it—consequently cambium, phloem and surrounding tissues are gradually pushed outwards and for this primary tissues get crushed. But the primary xylem remains more or less intact in or around the centre.

The cambium, here and there, also produces short strips of parenchyma cells in radial directions which pass through the secondary xylem and the secondary phloem—these strips of parenchyma are known as *secondary medullary rays or secondary rays.*

(c) Formation of Annual rings—Formation of annual rings, growth rings or growth layers takes place often by the periodical activity of the cambium. This periodical activity of the cambium is due to variations in

environmental conditions. Generally the periodicity in the activities of the cambium is seasonal, i.e. cambium is more active in spring or during the active vegetative season producing greater amount of xylem vessels

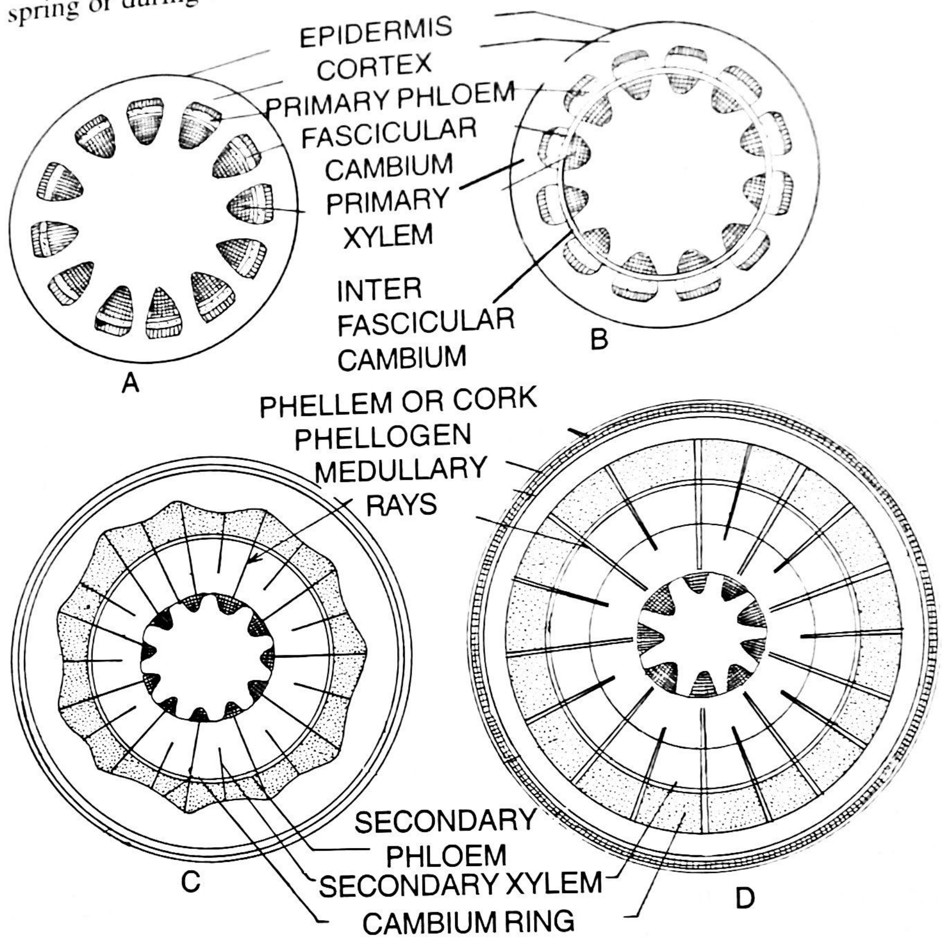

Fig. 7.1 Secondary growth in stem showing different (A-D) stages (diagrammatic).

with wider cavities. Again in winter or during the inactive period, the cambium is less active producing smaller amount of xylem vessels with narrower cavities. The wood thus formed in spring is called *spring wood* or *early wood* and that formed in winter is called *autumn wood* or *late wood*. In a transverse section of the stem, these two types of wood appear together as a concentric ring known as *annual ring* or *growth ring*. It is to be noted that each annual ring corresponds to one year's growth—hence the age of a plant can be determined roughly by counting the total number of annual rings.

◆ II. Growth in Extrastelar Region :

The new i.e. secondary tissues formed by the cambium in the intrastelar region exerts some pressure on the peripheral tissues of the stem—as a result epidermis becomes stretched more or less and often ruptured here and there, the cortex is also affected in a similar way. Hence to replace or to protect the peripheral tissues like epidermis, cortex, etc. from degeneration a strip of secondary lateral meristem called *cork-cambium* or *phellogen* arises to that region to give rise to secondary tissues. The cork-cambium usually originates in the hypodermis, or in the epidermis itself or in innermost region of the cortex—the cells of these regions become meristematic and form a thin strip of cork–cambium. This cork-cambium by meristematic activity cuts off new cells on both sides forming the *secondary cortex* or *phelloderm* on the inner side and *cork* on the outer side.

The cells of the secondary cortex (phelloderm) are arranged in a few rows and are added on to the primary cortex; they are parenchymatous and living, they often contain chloroplasts and carry on photosynthesis; in some cases these cells are thick-walled.

Cork is also known as *phellem*. The new cells cut off by the cork cambium on the outer side are more or less rectangular and become suberised. *Cork* cells are dead, thick-walled and suberised; they have no intercellular spaces.

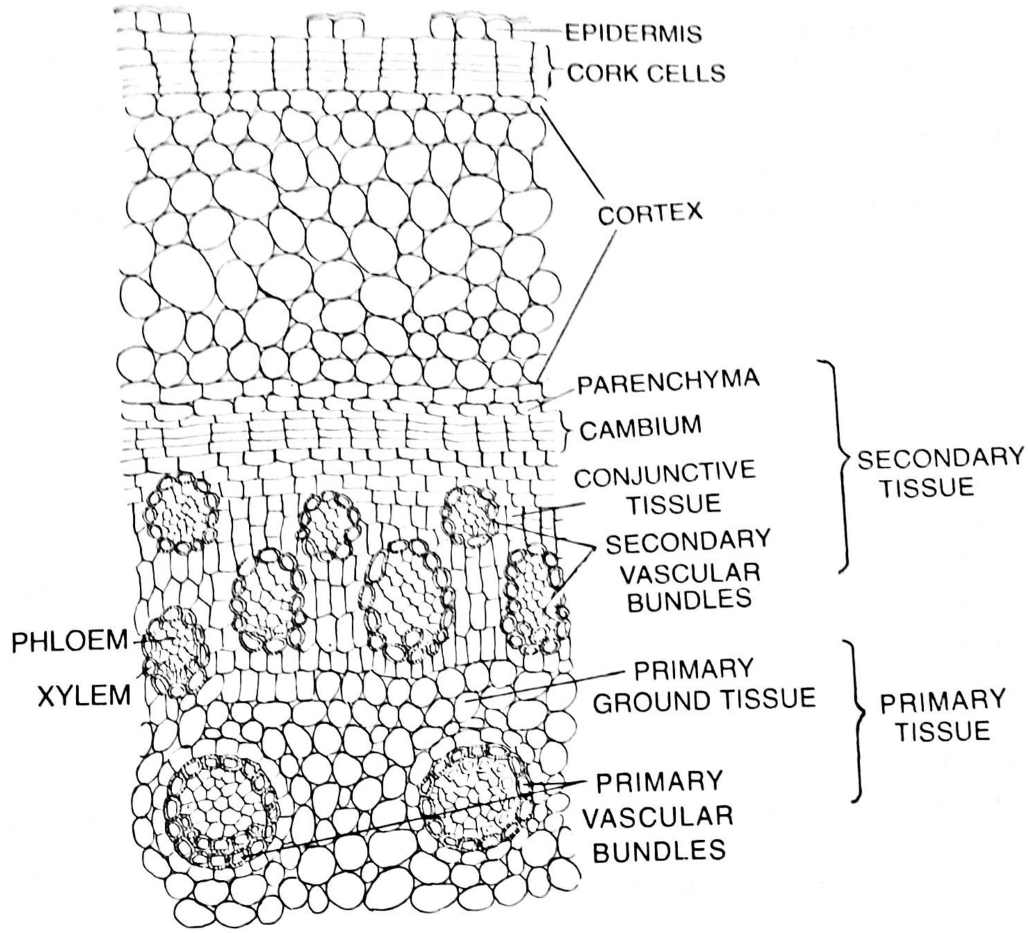

Fig 7.2 T.S. of a portion of *Dracaena* stem showing secondary growth.

Phellem, phellogen and phelloderm—these three together constitute a new secondary tissue in the cortex and are known as *periderm*.

As a result of the repeated activities of the phellogen in different regions of the underlying tissues, *bark* (dead tissue lying outside the phellogen) of considerable thickness is produced.

Lenticel formation in periderm takes place due to the activity of phellogen ; lenticels are so-called pores of special form having cells with intercellular spaces. They are developed in the bark through which gaseous exchange takes place. These pores i.e. lenticels originate first just beneath the stomata and later by the growth and formation of loose cell groups (complementary cells) by the phellogen, epidermis is ruptured and complementary cells are exposed forming a space or pore.

● 7.3 Secondary growth in monocot stem (Fig. 7.2) :

In monocotyledonous stems, normally no secondary growth takes place as the vascular bundles are closed i.e. *without cambium*, hence the vascular system is entirely composed of primary tissues. But in some herbaceous and tree-like woody (i.e. arboreal) monocotyledonous plants belonging to the families Liliaceae (e.g. *Aloe, Dracaena, Yucca, Cordyline*), Agavaceae (e.g. *Agave*), etc. secondary increase in thickness by the activity of the secondary cambium (which is entirely a secondary meristem) takes place.*

* In most arborescent palms, similar type of secondary growth is also noted (Cutter, 1978).

the activity. Cytokinins, which are considered to stimulate cell division, may also affe (Cutter, 1978). It has been shown experimentally by Digby and Wareing (1966) that the highest rate of cambial activity in *Acer* sp. is attained in the presence of auxin, gibberellin and kinetin together.

There are various methods for determining the cambial activity. The method by which the bark may be peeled is used as an indication of cambial activity. There is another method based on anatomical studies of cross-sections cut in the region of the cambium and the tissues adjacent to it; in this method the number of cell layers of still undifferentiated xylem elements is taken as an indication of the rate of cambial activity. The most recent method is that in which both the rates of cell division and of cell differentiation can be determined by the application of radioactive carbon to photosynthesising plants (Fahn, 1982). In case of active cambium, the radioactive carbon is incorporated in the newly formed cells where it can be detected by autoradiographic techniques.

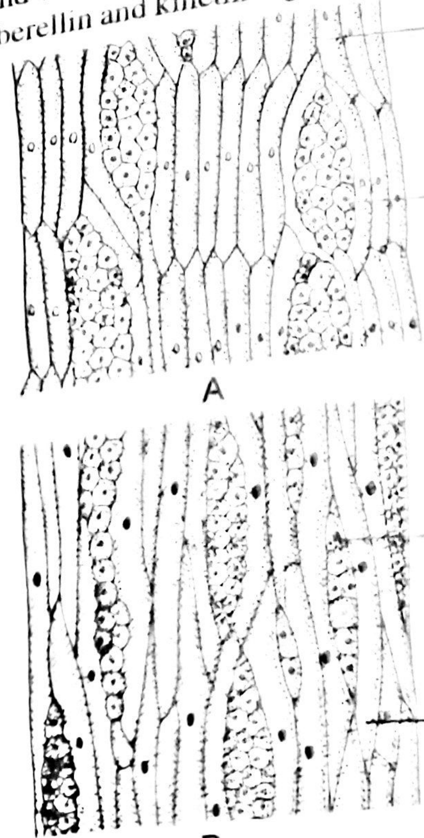

Fig. 7.10 Diagrams of fusiform initial and ray initial in l.s. of cambium. A– storied or stratified cambium and B–non-storied or non-stratified cambium.

● 7.8 Periderm—its structure, origin and function :

Periderm is a protective layer of tissue of secondary origin. It replaces the epidermis (which dies and is shed) of stems and roots having continual secondary growth. The development of the secondary vascular tissue is generally accompanied by the formation of cork. This cork tissue is actually termed the periderm. Periderm formation takes place mainly in woody dicotyledons and gymnosperms, sometimes in monocots and in older parts of stems and roots of herbaceous dicot plants. Periderm develops near injured or dead tissue and also along exposed surfaces after abscission of plant organs. Periderm is formed by a type of lateral meristem called the *phellogen* or *cork cambium*.

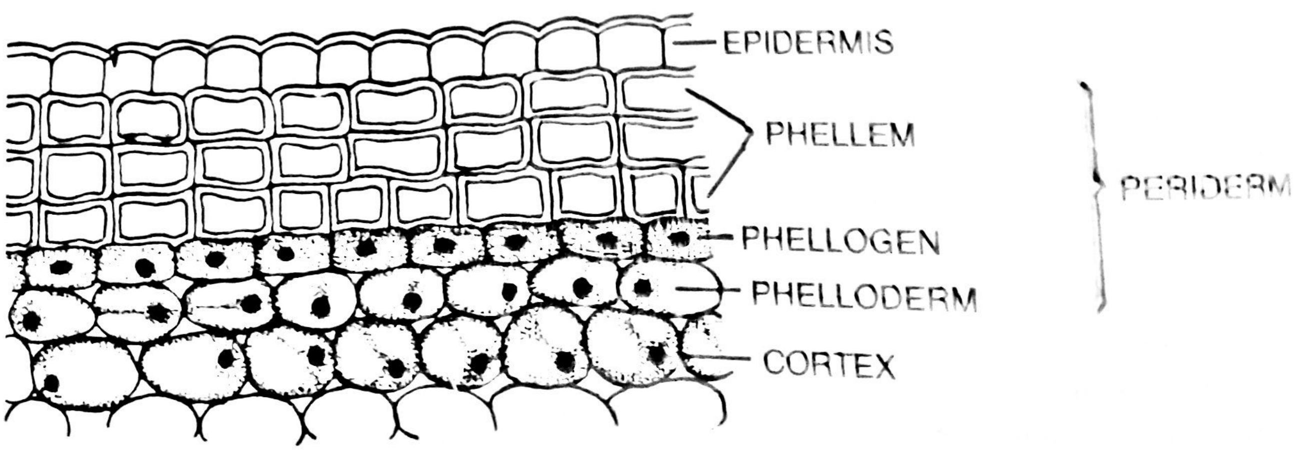

Fig.7.11— Diagram showing periderm formation.

Structure of Periderm—Periderm usually consists of three layers of tissues, viz. (a) the *phellogen* or *cork cambium*—the initiating meristem, (b) the *phellem* or *cork*—the protective tissue formed towards outside i.e. centrifugally by the phellogen and (c) the *phelloderm*—layer of living parenchyma tissue formed towards inside i.e. centripetally by the phellogen.

(a) *Phellogen*—Structure of the phellogen is simpler than the vascular cambium ; this type of cambium consists of one type of cell. In longitudinal section cells look rectangular, polygonal or irregular in outline.

while in cross section phellogen cells appear as rectangular and radially flattened structure. Intercellular spaces are absent in the phellogen cells except in those regions where lenticels develop. The phellogen cells contain within the protoplast variously sized vacuoles, sometimes chloroplasts and tannins. The phellogen is a lateral *secondary* meristem which originates from permanent living cells of the epidermis, cortex or phloem cells as a result of meristematic activity, and it produces tissues that comprise part of the secondary plant body.

The phellogen results in an increase of the diameter of the plant axis by periclinal divisions in its cells. The phellogen divides periclinally to give radially seriate files of cells, those towards the outside differentiate as phellem or cork and those towards the inside as phelloderm or secondary cortex.

(b) *Phellem*—Cells of the phellem are commonly known as cork cells. The cells are more or less prismatic in shape although they are polygonal in tangential section and are flattened radially in cross-section. In cross-section, the cork cells are generally seen to be arranged compactly in radial rows that are devoid of intercellular spaces. The cork cells become non-living at maturity. The walls of cork cells vary in thickness and are suberised; sometimes they are non-suberised, called *phelloid cells*. The suberin occurs as distinct lamella covering the original primary cellulose wall—which may be lignified. The walls of cork cells may be coloured (yellow or brown) or cavities of cork cells may contain coloured materials. According to Eames and MacDaniels (1947), of the various types of cork cells, two types are common e.g. (1) one type having thin-walled, empty and radially elongated cells like the tissue of bottle cork type and (2) the other type having thick-walled and radially thin cells with the lumen (cavity) filled with coloured materials. The prevention of water loss is mainly secured by cork cells.

(c) *Phelloderm*—Cells of phelloderm are living with non-suberised cellulosic wall just like cortical parenchyma cells. Cells are loosely arranged and pitted. Phelloderm cells differ from cortial parenchyma cells in their definite arrangement in radial rows. Phelloderm cells may contain sometimes sclereids and other special cells. In some plants phelloderm cells contain chloroplasts. Function of phelloderm cells is both photosynthetic and storage of carbohydrates.

Origin of Periderm—Appearance of first periderm generally takes place during the first year of growth of stem or root—deeper periderm may appear subsequently in the same year or may not appear.

The origin of first periderm takes place commonly in the sub-epidermal layer (i.e. in hypodermis, cortex, etc.) or in the epidermis itself. In roots the first periderm originates in the pericycle just beneath the endodermis; where the origin is hypodermal, the epidermis is ruptured and it disintegrates very soon.

The first phellogen or cork cambium is initiated either uniformly around the radius of the axis or in localised areas and which later becomes continuous by lateral expansion of the phellogen due to meristematic activity. Subsequent periderms appear as overlapping layers. Initiation of phellogen is due to periclinal division of various types of cells, e.g. epidermal, sub-epidermal parenchyma or collenchyma cells or parenchyma cells of the pericycle or phloem depending upon the position of phellogen—initiating cells are all living and therefore potentially meristematic. The phellogen initials divide periclinally and produce the phellem and phelloderm outwardly and inwardly respectively. Phellogen of first periderm produces more cells (phellem) outwardly than phelloderm, the cells of which are sometimes restricted even to a single layer.

Function—The main function is to protect the underlying tissues from drying out by the corky and suberised layers. The prevention of water loss is also secured by cork cells.

7.9 Polyderm, Rhytidome, Storied cork, etc. :

(a) *Polyderm*—It is a special type of protective tissue which is formed in the pericycle of the root and underground stem of certain plants belonging to the families Rosaceae, Myrtaceae, Onagraceae, etc. Polyderm consists of two alternating tissue-layers; in one, the layer is composed of one-cell thick, endodermis-like and partly suberised cells and in the other, the layer is made up of several-cells thick non-suberised cells. At the ... Casparian strips appear on the wall, which, in