

ANATOMICAL STRUCTURE OF PRIMARY BODY OF THE PLANT AXIS

EPIDERMIS

The epidermis constitutes the outermost layer of cells of the plant axis. The primary function of the epidermis is water regulation and mechanical protection. It is the first line of defense against biological pests (Levin, 1973; Mabry et al., 1977; Rodriguez et al., 1984). Aerial epidermis is resistant to water movement (loss) in contrast to the root epidermis which facilitates movement (absorption). In stem, epidermis performs the function of the transpiration and gaseous exchange through stomata and protects the plant from excessive solar radiation (Martin and Juniper, 1970). Because of compact arrangement of the cells and the presence of the relatively tough cuticle, the epidermis also offers mechanical support and adds stiffness to the stem (Niklas and Paolillo, 1997). The root facilitates water absorption as they are embedded in the soil or some similar substrate and are able to extract water from the soil because the protoplasm of root is drier than the soil (their water potential is more negative). Epidermis in the shoot arises from the outermost layer of the apical meristem while in the root the epidermis may have a common origin with cells of the root cap or differentiate from the outermost cell layer of cortex (Clowes, 1994).

In stem epidermis consists of a single layer of cells and covered by a thin layer of cuticle. In some species, the cuticle has complex patterns of striations, bumps and wrinkles (Stace, 1965; Van Staveren and Baas, 1973; Wilkinson, 1971). Epidermis shows presence of stomata and several types of trichomes. Trichomes are highly variable

epidermal appendages of diverse types and have diverse functions. Trichomes vary widely in structure within families and smaller groups of plants; they are sometimes remarkably uniform in a given taxon and have been used for taxonomic purposes (Uphof and Hummel, 1962; Theobald et al., 1979).

Trichomes are divided into two types - nonglandular and glandular trichomes.

Nonglandular trichomes

Nonglandular trichomes may be unicellular or multicellular. Unicellular trichomes are extremely common. They consist of a single cell that project above the surrounding surface. Multicellular trichomes may be uniseriate, biseriate or multiseriate. They may be long or short with few or many cells and they may be branched or unbranched. Some of the branched trichomes are stellate hairs, peltate hairs, candelabriform hairs and scale or squamiform hairs. The non glandular trichomes can along with the cuticle and waxes protect against excessive sunlight. As they die and dehydrate, their walls become more refractile and scatter light. Such a structure is also a deterrent against insects because the hairs can tangle the feet or impale the insect; being dead and empty. These trichomes are of little nutritive value to the insect. Other trichomes absorb water and salts (Benzing and Pridgeon, 1983; Pridgeon, 1981).

Glandular trichomes

Glandular trichomes are specially modified for the secretory nature. The glandular trichomes secrete water, salt, nectar, mucilage, terpenes, adhesive, digestive enzymes and irritants that sting. The glandular trichomes consist of a basal cell, stalk cell and head cell (or secretory cell). Sometimes surrounding epidermal cells are modified into collecting

cells. The secretory region may be isolated by casparian strips so that the secretory product cannot flow back into the plant apoplastically. Glandular trichomes are covered with cuticle (Cutler et al., 1982). In many cases secretory product accumulates below the cuticle, which is lifted away from the cellulosic portion of the wall. In other cases the cuticle tears and the secretion is liberated immediately.

Root epidermis is simpler in structure and shows absence of stomata and trichomes. The epidermal cells of root are thin walled and show presence of root hairs. Root epidermis is usually devoid of cuticle (Bonnett and Newcomb, 1966; Juniper and Clowes, 1965; Juniper and Roberts, 1966). Sometime the outermost cell walls including the root hairs undergo cutinization (Guttenberg, 1940; Scott et al., 1963). Root hairs are adapted to the efficient uptake of water and nutrients (Russell, 1977). The region of the root hairs is usually restricted to one or a few centimeters from the root apex. Root hairs are absent close to the apical meristem and they usually die and dry out on the more mature portion of the root. Certain herbaceous plants and especially water plants show absence of root hairs. Root hairs are formed by the unequal division of the epidermal cells of piliferous region. The short cell (the trichoblast or piliferous cell) grows out as the root hair. However, in some plants every root epidermal cell grows out as root hairs. Root hairs are usually unicellular rarely multicellular as in *Kalanchoe fedtschenkoi* (Popham and Henry, 1955). They may become forked (Guttenberg, 1968). Root hairs walls may become lignified and suberized (Artschwager, 1925; Cormack, 1949).

The epidermis of root is usually uniseriate but in the aerial roots of plants

belonging to the family Orchidaceae and in the epiphytic and tropical genera of the Araceae, epidermis is multiseriate and is specialized to form velamen.

CORTEX

The cortex is the region between the epidermis and the vascular cylinder (stele). Cortex is typically composed of uniform mass of parenchyma. Innermost layer of the cortex is endodermis.

In root, cortex is composed of thin walled parenchyma cells which often contain starch grains. The root cortex is usually wider than the stem cortex and therefore plays a larger role in the storage. Schizogenous intercellular spaces(which appear in early ontogenetic stages) are very common in the root cortex. Water and dissolved solutes easily move between the cortical cells in the intercellular space. In certain plants(such as the Gramineae and Cyperaceae),large lysigenous intercellular spaces often develop in addition to the schizogenous ones. The parenchyma cells of root cortex usually lack chlorophyll. But in the roots of certain water plants and in the aerial roots of most epiphytes chlorophyll is present. Secretory cells, resin ducts and laticifers are found in the root cortex of different plants. Roots, where secondary growth is absent, cortex may live as long as the rest of the root and may develop large masses of sclerenchyma. Collenchyma is rarely found in roots (Guttenberg, 1940).

Stem cortex is composed of thin walled parenchyma with intercellular spaces and also contains various other types of cells like sclerenchyma, collenchyma and laticifers. In the stem of some plants, specialized photosynthetic parenchyma (chlorenchyma),

sclerenchyma or collenchyma can form a distinct subepidermal hypodermis or sclerenchyma may form a sheath around the vascular bundles.

ENDODERMIS

Endodermis is always a single layered cylinder of cells without intercellular spaces that line the inner boundary of the cortex and outer boundary of stele. It is universally present in roots. However, three species of angiosperm are known to lack a root endodermis viz. *Canarium commune*, *Tinospora crispa* and *Nyssasylvatica* (Guttenberg, 1968).

Endodermal cell walls are distinguished by the presence of casparian thickening which appear as strips in the radial and cross walls of the endodermal cells. These strips are integral parts of the primary wall and the middle lamella in which suberin and lignin are deposited (Van Fleet, 1942). The casparian strips prevent inward flow of water and nutrients through the apoplast (Clarkson and Robards, 1975).

In many angiosperms, the endodermis remains in the primary form and is shed together with the cortex with the development of secondary thickening and periderm. However, in some angiosperms in which there is no secondary growth, an almost continuous lamella of suberin develops on the inner side of the entire primary wall, including casparian strips. This lamella characterizes the second stage of development of the wall and in the third stage a layer of cellulose is laid down centripetally on the inside of the suberin cellulose. This layer may reach a very considerable thickness on the radial walls and on the inner tangential walls of the endodermal cells. This type of endodermal

cell is common in the roots of most monocotyledons (Guttenberg, 1943; Clark and Harris, 1981). These thickened endodermal cell walls may become lignified.

The endodermal cells opposite xylem often have casparian strips only. These cells are termed passage cells as they are thought to provide passage for substances between the cortex and vascular cylinder. The passage cells may remain unaltered throughout the entire life of the root or they too may develop thick secondary walls as do the other endodermal cells.

A true endodermis is rarely present in angiospermous stem but there are a number of angiosperms, mostly herbaceous stem which develop an endodermis with casparian strips (Guttenberg, 1943; Courtot and Bailland, 1960; Van Fleet, 1961). Underground rhizomes have an anatomically identifiable endodermis more frequently than the aerial axes. Sometime the endodermis develops casparian strips in herbaceous stem when the plant attains the flowering state (Warden, 1935).

The innermost cortical layer of young dicotyledonous stems usually contains many large starch grains. This layer has been termed as starch sheath and because of its position, it is considered to be homologous with the endodermis. Esau (1977) used the term “endodermoid.” In older stem regions this layer ceases to accumulate starch differentially or in some plants, develops casparian strips (Bond, 1931; Datta, 1945; Warden, 1935).

PERICYCLE

Next to the endodermis is a narrow region of parenchyma cells which is termed as

pericycle. It forms the outer boundary of stele. In roots, pericycle is clearly defined next to endodermis separating the cortex from the vascular tissue. Pericycle is usually a colorless parenchyma but in some plants fibres may also occur (Guttenberg, 1968; Warmbrodt, 1985). In most angiosperms, the pericycle is unistratose but in some (Gramineae, Palmae and *Salix*) it can be several layer thick.

In dicot roots that have secondary growth, the pericycle of root contributes to the vascular cambium. The cork cambium of roots also is derived from pericycle. In seed plants, the primordial of the lateral roots arise within the pericycle. In the monocots, the pericycle cells become sclerified in older region of the roots. In the roots of certain water plants and parasites the pericycle is absent.

In stems there is no well-defined layer separating the cortex from the vascular tissues, for the protophloem differentiates next to the innermost cortical layer. In some dicots stems, a more or less continuous cylinder of fibres occurs on the periphery of the vascular cylinder. The fibres may originate from the same meristem as the phloem (eg. *Pelargonium*) or from tissue outside the phloem but inside the starch sheath eg. *Aristolochia* and *Cucurbita* (Blyth, 1958; Carothers, 1959; Mourré, 1958). Thus in some stems nonphloic tissue occurs between the cortex and the phloem. This kind of tissue was used by Van Tieghem (1882) when he introduced the concept of the pericycle, but later the concept came to be applied to all stems and roots. In many seed plants, the term pericycle refers to the outermost part of the phloem (Metcalf and Chalk, 1950).

The parenchyma cells of the pericycle share the function of storage with similar cells in the other regions.

ARRANGEMENT OF VASCULAR TISSUES

In roots, xylem and phloem are arranged in radial manner while in stem phloem is external to xylem forming conjoint and collateral vascular bundles. Xylem is exarch in roots and endarch in stems.

The number of protoxylem groups in the dicot roots may be one, two, three, four, five, six and is expressed by the terms monarch, diarch, triarch, tetrarch, pentarch, hexarch respectively and in monocot roots which have many protoxylem groups the term polyarch is used. A correlation exists between the diameter of the vascular cylinder and the number of protoxylem groups and the presence or absence of pith. In dicots root, pith is small while in monocots pith is large.

In monocot stems vascular system usually consists of closed (cambium absent) bundles that are scattered throughout the ground tissue of the stem as seen in a T. S. of stem. In monocots xylem is V-or U-shaped as seen in cross section. In the case of V-shaped xylem, the phloem groups are situated at the free ends of the xylem arms. While in U-shaped xylem, the phloem is surrounded on the three sides by xylem. The primary bundles e.g. *Convallaria majalis*, *Acorus*, some genera of the Xanthorrhoeaceae as well as in the secondary bundles of some monocots like *Aloe arborescens*, *Dracaena*, *Cordyline* and others, the xylem surrounds the phloem. Such bundles are amphivasal bundles. In the bundles when the phloem surrounds the xylem are amphicribal bundles. Amphicribal bundles occur in unusual situations in the dicots, as medullary bundles in *Begonia*, *Mesembryanthemum*, *Rheum* and *Rumex*.

In dicotyledonous stem, the vascular bundles are open and form a ring. In some

dicotyledonous families eg. Solanaceae, Cucurbitaceae, Asclepidaceae, Apocynaceae, Convolvulaceae and Compositae internal phloem is also present. The internal or intraxylary phloem may be present as separate strands on the border of the pith as in *Lycopersicon* or it may be in close contact with the inner side of the xylem as in the stem of the Cucurbitaceae and Myrtaceae. The internal phloem may differentiate from procambium or from partly differentiated parenchyma cells (Fukuda, 1967). A vascular bundle in which the intraxylary phloem is in close contact with xylem is termed as a bicollateral bundle.

Medullary and cortical bundles present on the inside and outside of the stele respectively are found in certain plants (Bary, 1877; Eames and MacDaniels, 1947; Metcalfe and Chalk, 1950). These bundles are associated with stems of both anomalous and normal structure. Medullary bundles occur in numerous dicotyledonous families eg. in the Amaranthaceae (Wilson, 1924), Cactaceae (Boke, 1961; Gibson and Nobel, 1986; Mauseth, 1988), Chenopodiaceae, Melastomataceae (Lignier, 1887), Nyctaginaceae, Piperaceae and Polygonaceae (Davis, 1961; Howard, 1979; Pant and Mehra, 1964b).

Cortical bundles are less common and are known to occur in Melastomaceae, Proteaceae, Araliaceae and Calycanthaceae. Cortical bundles are often leaf traces which descend through the cortex for some distance before entering the stele eg. as in *Begonia* and *Casuarina*.

In certain families, such as the Chenopodiaceae, Amaranthaceae, Nyctaginaceae, Salvadoraceae, phloem is also present within the secondary xylem. This type of phloem

is called interxylary phloem or included phloem.

PRIMARY VASCULAR TISSUES

Primary xylem and phloem are formed from procambium, differentiated into protoxylem and metaxylem and protophloem and metaphloem respectively. The protoxylem tissues are the first to differentiate. If the xylem is exarch, the protoxylem appears on the outer margin of the xylem system or strand, the metaxylem at or near the center. In the endarch xylem the relative positions of the two parts of the xylem are reversed.

The first protophloem consists of sieve cells or sieve tubes distributed among procambium cells. Companion cells are rare or absent. Later, the procambium cells around these first maturing cells differentiate as parenchyma cells and fibres. The metaphloem is a complex tissue with well-developed cells of all types like sieve cells or sieve tubes, companion cells, parenchyma cells and sclerenchyma in the form of fibres or sometimes sclereids. The sieve elements of the metaphloem are larger than those of the protophloem and their sieve areas are much more distinct (Esau, 1969). In the dicots, both non-conducting parenchyma and companion cells are present, interspersed with the sieve tubes, although fibres are lacking (Esau, 1965a). In the monocots, non-conducting parenchyma is typically absent and the metaphloem consists of sieve tube members and companion cells in a regular array.

The protoxylem often contains more parenchyma than tracheary elements; either tracheids or vessel elements may be present but fibres are absent. The metaxylem is

usually more complex, having more conducting cells and less parenchyma; fibres may also be present. The protoxylem has secondary wall thickenings in the form of ring (annular) or helices (spiral). In metaxylem and secondary xylem, the helical bands are joined in certain regions giving the appearance of a ladder. Such thickening is known as scalariform thickening. Secondary wall thickenings in the form of a network are known as reticulate thickenings. In vessel elements, perforations are usually present on the end walls but sometimes they are subterminal or lateral in position. The region of the wall where perforations occur is known as perforation plate. Two types of perforation plates are present in angiosperm-simple and multiple. Multiple perforation plates may be scalariform, reticulate or foraminate.

Spiral and annular thickenings are much fewer in the protoxylem of roots than in that of stems, probably because very few xylem elements mature during the elongation stage, developing rather in the zone just behind this, where there is no elongation. In the stem the function of annular and spiral thickened elements is to conduct water and nutrients to the growing tip. The root tip, on the other hand, is surrounded by moist soil and absorbs water and nutrients directly by the root hairs.

The primary phloem of angiosperm roots consist of sieve tubes, companion cells and parenchyma and differs in no fundamental way from that of stems of the same species.

PITH

The pith is a cylindrical body of tissue in the center of the axis, enclosed by the vascular tissues. In stem its outer surface is furrowed more or less deeply by the inwardly projecting strands of protoxylem and ridged in some plants by ray-like extensions between bundles and by projections where its tissues extend out through leaf and branch gaps.

The pith is made up of parenchyma. Which are arranged loosely with intercellular spaces. In shape, the cells of pith vary greatly but they are mostly isodiametric or cylindrical with thin cellulose walls. Sclerenchyma is rarely present but when it does occur, it may be composed of either sclereids or even more rarely fibres located on the edge of the pith close to the vascular bundles as in Araliaceae, Malvaceae and Polygonaceae (Solereeder, 1908).

In kind of cells, intercellular spaces, secretory tissues and cell content, the pith is usually closely similar to the cortex of the same plants, except that protective, supportive and photosynthetic cells are scarce or lacking in the pith.

If marked radial increase is taking place at the same time, prominent “hollow pith” is formed, with the broken cell walls lining the cavity. This condition is common among herbs but rare in stem of woody plants. Where the destruction is less extensive, cavities or canals of various extent and shape are formed.

As parenchyma, the pith can have a role in storage, although it is often too small to be very significant, except in some tubers such as potatoes, where it constitutes almost the entire stem (Artschwager, 1924; Reed, 1910).

SECONDARY GROWTH IN PLANT AXES

Primary growth chiefly increases the length of the axis and adds the appendages while secondary growth increases the diameter of the axis. Primary vascular tissues are formed from the procambium strands or cylinder. In the plants, where there is no secondary growth, all the cells of procambium strands mature to form primary xylem and phloem. But in plants (dicots and gymnosperms) in which secondary growth occurs a part of procambium remains meristematic and gives rise to the proper cambium.

In roots, the formation of the cambium differs from that in stems because of the radial arrangement of the alternating xylem and phloem strands. Here the cambium arises as discrete strips of tissue in the procambial strands inside the groups of primary phloem. Later, by lateral extension the strips of cambium are joined in the pericycle opposite the rays of primary xylem. Thus the cambium in roots, in its early stage of development does not form a symmetrical cylinder, but rather (as seen in cross section) a band of tissue that curves outward around the ends of the xylem rays and inward inside the strands of phloem.

SECONDARY GROWTH IN DIFFERENT GROWTH FORMS

The strip of cambium that arises within the bundle of primary vascular tissue of stem is called as fascicular cambium. The strips of fascicular cambium usually become joined by additional strips of cambium which constitute the interfascicular cambium. The interfascicular cambium develops from the interfascicular parenchyma. Cambium produces secondary xylem towards the innerside and secondary phloem towards outside. Details of origin and activity show variation in different growth forms. Commonly three patterns have been observed in dicots -

1. The primary vascular tissues form an almost continuous vascular cylinder in the internodes (the interfascicular regions are very narrow) and the secondary vascular tissues do the same.
2. The primary vascular tissues form a system of strands but the secondary vascular tissues arise as a continuous cylinder (eg. *Salix* and *Prunus*) and many other herbaceous and woody dicotyledons.
3. The primary vascular tissues form a system of strands, the interfascicular cambium produces only ray parenchyma and therefore the secondary vascular tissues also appear as strands eg. Vine types of stem, as *Aristolochia* and *Vitis*. In some herbaceous dicotyledons with secondary growth, the interfascicular cambium may produce only fibres or only sclerified parenchyma on the xylem side (*Medicago* and *Salvia*) or the secondary growth may be so small in amount that it remains limited to the vascular bundles (*Trifolium* and *Cucurbita*).

The secondary growth of some dicot taxa deviates from the usual mode of secondary growth. The unusual is called as anomalous secondary growth. The stems with unusual secondary growth, which occur commonly in lianas, are referred anomalous ones or as presenting cambial variants (Eames and MacDaniels, 1953; Sajo and Castro, 2006). The anomalous or unusual structure may be a consequence of (1) a cambium of normal type which gives rise to unusual arrangements of secondary xylem and phloem, or (2) a cambium which itself is abnormally situated and so gives rise to abnormal arrangements of tissues or (3) the formation of accessory or additional cambial zone (Eames and MacDaniels, 1953; Cutter, 1969).

SECONDARY XYLEM

The secondary xylem is composed of two systems, the axial (vertical) and the radial (horizontal) system. The radial system comprises of the xylem rays and the axial system comprises of the tracheary elements, fibres and wood parenchyma.

TRACHEARY ELEMENTS

Tracheary elements consisting of tracheids and vessels are chiefly involved in the conduction of water and solute from root to other parts of plant body. Both are more or less elongated cells that have lignified secondary walls and are non-living at maturity but differ in their detailed structure and arrangement. Tracheids are long and imperforate elements with tapering end walls and have pit-pairs on their common walls. Tracheids are always arranged in such a way that contiguous cells overlap at least over the tapering portions. Over these tapering areas the pits are abundant. While a vessel is built of

numerous vessel members that are joined one to other by their perforated end walls called perforation plates. Vessel members also have pits on their lateral walls. Vessels show two types of perforation plate -

Simple perforation plate - Perforation plate has a single perforation.

Multiple perforation plate - Perforation plate has several perforations. Multiple perforation plates are of three types - Scalariform, reticulate and foraminate perforation.

Secondary walls of tracheary are characterized by presence of pits. Pits are commonly simple, half-bordered and bordered. In certain dicots woods, the pits are wholly or partly lined with minute branched protuberances on the secondary wall (Jansen et al., 1998, 2001). These pits are called vestured pits.

INTERVASCULAR PITS

Pits in the walls of vessels vary in shape, size and arrangement especially in relation to the type of adjoining cell. The intervacular pits between contiguous vessels occur in pit-pairs and are usually abundant. If the neighboring cell is fibre then the pits between the vessels and fibres are few and very small in size or there may be no pits. The pits between the tracheary elements and parenchyma are commonly half-bordered, bordered pits on the tracheary element side but simple indentations of the primary wall on the parenchyma cell side.

Intervacular pits between the contiguous vessels are of three main types - scalariform, opposite and alternate. Scalariform pitting consists of elongated or linear pits with their long axes orientated transversely across the length of the elements. Opposite pitting is multiseriate and the individual pits in each row tending to be opposite those of

the adjacent rows. In alternate pitting, pits are closely placed and arranged in diagonal rows and tend to be hexagonal in shape.

ARRANGEMENT OF VESSELS

The arrangement of the vessels in the secondary xylem of dicotyledons is a characteristic feature and is used in the identification of species. The wood in which vessels are more or less uniform in size and distribution throughout the growth ring is known as diffuse porous wood. When the wood contains vessels of different diameters and in which those produced at beginning of the season are distinctly larger than those of the late-wood, the wood is known ring-porous wood. When woods show an intermediate condition between ring-porous and diffuse porous wood that is called as semi-ring porous or semi-diffuse porous wood.

Vessels may occur as solitary vessels which may be circular or elliptical as seen in cross-section or they may appear in groups of two or more forming multiple vessels. Multiple vessels may be in clusters or radially arranged. In some woods vessels show a distinctly radial or oblique pattern that is characteristic of taxonomic groups in which they occur.

FIBRIFORM VESSEL ELEMENTS

The term fibriform vessel element was given by Woodworth (1935) for slender fusiform vessel elements, which are often longer than the ordinary vessels elements they accompany in any given wood in which they occur. As the tips of these cells are pointed the perforations are subterminal and often appear lateral thereby (Carlquist, 1984a).

VASICENTRIC TRACHEIDS

Vasicentric tracheids are imperforate cells that bear fully bordered pits like the pits of vessel elements in the woods in which they occur. They are distributed around vessels and vessel groups and are somewhat longer than vessel elements in any given wood. Vasicentric tracheids tend to be wider than the remaining imperforate tracheary elements and more densely pitted than the remaining imperforate tracheary elements in woods in which they occur (Carlquist, 1984a).

VASCULAR TRACHEIDS

Vascular tracheids are described as vessel elements which are so narrow that they lack perforation plates. Vascular tracheids tend to be the same length as the vessel elements in any given sample but are appreciably shorter than the libriform fibres with which they are associated. They occur in woods that have sharply demarcated growth rings and the vascular tracheids always occur in latewood only (Carlquist, 1984a).

WOOD FIBRES

Fibres are long cells with secondary lignified walls. The walls of fibres are usually thicker than the tracheids in the same wood. Two principal types of xylem fibres are recognized; the fibre-tracheids and libriform fibres. If both occur in the same wood, the libriform fibre is longer and commonly has thicker walls than the fibre-tracheid. The fibre-tracheids have bordered pits with cavities smaller than the pit cavities of tracheids or vessels in the same wood. These pits have a pit canal with a circular outer aperture and an elongated or slit-like inner aperture.

Both types of fibres may be septate. Septate fibres usually retain their protoplasts in the mature active wood, where they are concerned with the storage of reserve materials.

WOOD PARENCHYMA

Two types of parenchyma are found in the secondary xylem—the axial parenchyma and ray parenchyma. The cells of the ray and axial parenchyma are interconnected forming a continuous system of living cells. The ray parenchyma cells originate from ray initials of the cambium while those of axial parenchyma develop from the fusiform initials. The cells of the axial parenchyma may be as long as the fusiform initial from which they are formed or much shorter as a result of transverse division prior to differentiation. The shorter axial parenchyma cells are the more common.

The parenchyma of the xylem serves to store reserve materials such as starch and fats. Tannins, crystals, silica bodies and other substances are also frequently found in many of these cells (Ter Welle, 1976; Richter, 1980). Sometimes the parenchyma cells containing crystals divide so that chambers, each containing one crystal are formed (Chattaway, 1955, 1956).

In many plants the cells of both types of wood parenchyma form protuberances which penetrate through the pits into the vessels after they become inactive or into the vessels of xylem tissue that has been injured. These outgrowths are termed tyloses (singular: tylosis). The nucleus and part of the cytoplasm of the parenchyma cells, from which the tylosis is formed, enter the tylosis. Tylosis may divide. Although tylosis formation is considered to be a normal phenomenon, in many species it has also been

found to be induced by mechanical injury and by disease (Zimmermann, 1979).

AXIAL WOOD PARENCHYMA

The amount of the axial parenchyma and its distribution varies in the different dicotyledonous species. In some species, there is very little axial parenchyma or it is entirely absent; while in other it constitutes a very large portion of the wood. There are two basic types of axial parenchyma - apotracheal and paratracheal parenchyma.

Apotracheal parenchyma

The parenchyma is normally independent of the vessels though it may come in contact with them here and there. Apotracheal parenchyma is subdivided into the following variations -

- 1. Diffuse parenchyma** - When the apotracheal parenchyma is in the form of small uniseriate strands or single cells scattered irregularly among the fibres.
- 2. Banded parenchyma** - When in a cross section of the wood, the axial parenchyma is seen to form bands, eg. *Carya*, *Diospyros*. Banded parenchyma may be mainly independent of the vessels, associated with the vessel or both. They may be straight, wavy, diagonal, continuous or discontinuous and one to several cells wide. Parenchyma bands at the end of growth rings are called marginal bands.
- 3. Terminal parenchyma** - When parenchyma band is restricted to the end of a growth ring, eg. *Populus deltoides* and *Liriodendron tulipifera*.
- 4. Initial parenchyma** - When the parenchyma is present at the beginning of the growth ring. Initial parenchyma occurs in *Ceratonia*, *Zygophyllum* and *Spartinum*.

Paratracheal parenchyma

The parenchyma is distinctly associated with the vessels. The paratracheal parenchyma may be variously distributed. It is subdivided into the following variations -

1. Scanty paratracheal parenchyma - When the parenchyma does not form a continuous sheath around the vessels e.g. *Acer* and *Betula*.

2. Unilaterally paratracheal parenchyma - When the paratracheal parenchyma occurs on one side either external (abaxial) or internal (adaxial) of the vessel.

3. Vascentric parenchyma - When paratracheal parenchyma forms entire sheaths of different width around the vessels eg. *Fraxinus americana* and *Tamarix*. The shape of such sheath as seen in cross section of the wood may be circular or somewhat elliptical.

4. Aliform parenchyma - When sheath around vessel has lateral wing like extensions in transverse section eg. *Acacia cyanophylla* and *Cercis siliquastrum*.

5. Confluent parenchyma - When aliform parenchyma forms diagonal or tangential bands as seen in cross section eg. *Acacia raddiana* and *A. albida*.

RAY PARENCHYMA

The ray parenchyma cells are of two types - procumbent in which the longest axis of the cells is radial and upright in which it is vertical. Ray parenchyma cells may have primary walls only or may have secondary walls. Where secondary walls are developed the pits-pairs may be simple, half-bordered and sometimes bordered.

Rays which are composed of one kind of cell are called homocellular and those containing procumbent as well as upright cells are called heterocellular.

In angiosperms, rays may be one to many cells in height and one (uniseriate) to many (multiseriate) cells wide. Sometime several individual rays may be closely associated with one another which appear to be one large ray.

A number of dicots show absence of rays. In these plants cambium produces very little wood as in woody plant that appears herbaceous as well as in many xerophytes (*Sempervium arborenum* and *Staavia glutinosa*).

RADIAL VESSELS

The ray cells have perforations in their tangential walls and the terminal cells of a radial series of such elements are connected with a very narrow axial vessel or vascular tracheid through a perforation. These elements are called radial vessels and are found in uniseriate rays and uniseriate tails of multiseriate rays only. The shape of these radial vessel members similar to normal ray cells but they also have some characters that are typical for vessel members, like bordered vestured pits to contiguous parenchyma cells in an alternate pattern.