STRUCTURE, DEVELOPMENT AND REPRODUCTION IN FLOWERING PLANTS

The Leaf and Root System

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The Leaf

Leaf is a lateral appendage of the stem borne at a node and may bear a bud at its axil. Leaves are usually flat, thin, expanded structures that develop in an acropetal order on the stem. The common photosynthetic leaves are called foliage leaves. Leaves are essential for the plant as they perform several very important physiological processes like photosynthesis, transpiration and respiration.

The entire leaf axis is also called the Phyllopodium.

![Diagram of a leaf](image)

Diversity in size and shape of foliage leaf

A typical foliage leaf (Fig. 1) consists of three parts -

1. **Hypopodium or leaf base** - It is the point of attachment of the leaf to the stem. Lateral to it, leafy appendages, the stipules are found.

2. **Mesopodium or the petiole** - It is the stalk-like portion which connects the lamina with node of the stem.

3. **Epipodium or the leaf lamina or blade** - It is the anterior and flattened part of the leaf.

The entire leaf axis is called the phyllopodium.

Shape and size of a foliage leaf depends upon shape and size of its parts (i.e. leaf base, petiole, lamina). These structures show many variations resulting in overall variations in shape, size and structure of leaf.

**The leaf base (Hypopodium)**

Usually the leaf base is not demarcated from the petiole but when it gets modified into special structure then it can be easily identified. In many plants (e.g. *Mangifera indica*, *Mimosa pudica*, *Cassia fistula*, etc.) the leaf base is swollen and is called the pulvinus. In grasses, wheat, banana, etc. it becomes very prominent and winged, clasping and sheathing the part of internode just above the node and is called the sheathing leaf base. In banana the apparent stem is only a series
of sheathing leaf bases, one sheathing leaf base clasping the sheath of the next younger leaf and so on. The sheathing leaf base is called **amplexicaul** when it completely encloses the stem (e.g. wheat) and called **semi-amplexicaul**, if it incompletely encloses the stem (e.g. palm, banana). In some plants like *Symphytum*, the leaf petiole as well as the leaf base extend down the stem like a wing. This is known as a **decurrent** leaf base.

**Stipules**

Stipules are outgrowths arising from the leaf base. They protect the young axillary buds. Leaves are called **stipulate** if stipules are present and **ex-stipulate** if they are absent. The duration for which they remain attached to the leaf base varies from plant to plant. **Caducous** stipules fall off before unfolding of leaf (e.g. *Michelia champaca*). They are called deciduous when fall off soon after the leaf unfolds (e.g. *Cassia tora*) or **persistent** when remain attached to the leaf for the whole of its life (e.g. *Pisum sativum*). The stipules may be of following types -

1. **Free lateral** - Two, soft, thin and green stipules are present on either sides of the leaf base e.g. *Hibiscus* (China rose) (Fig. 2A).
2. **Adnate or adherent** - The two stipules are adherent to the sides of the petiole to a certain distance e.g. *Rosa* (rose) (Fig. 2B).
3. **Intrapetiolar** - Both stipules fuse by their inner margins to form a single compound stipule, e.g. *Gardenia* (Fig. 2C, D).
4. **Interpetiolar** - In this condition leaves are opposite decussate and superposed and stipules of two leaves fuse together e.g. *Ixora* (Fig. 2E).
5. **Ocloricate** - The two stipules fuse to form a hollow tube-like structure covering the internode up to a certain height, e.g. *Polygonum* (Fig. 2F).
6. **Convolute or bud scales** - The stipules become scaly and protect the vegetative bud, e.g. *Artocarpus* (Fig. 2G).
7. **Leafy or foliaceous** - The stipules are large leaf-like green structures. They also take up the function of foliage leaves, e.g. *Pisum* (Fig. 2H).
8. **Spiny** - Here stipules modify into spines and serve as a defensive armature, e.g. *Acacia* and *Zyzyphus* (Fig. 2I).
9. **Tendrillar** - The stipules modify into tendrils and help in climbing, e.g. *Smilax* (Fig. 2J).
In some plants like *Dolichos lablab*, the leaf is compound and stipule-like appendages are present at the bases of leaflets. These appendages are called **stipels**.

*The Petiole (Mesopodium)*

A leaf with a petiole or leaf stalk is called **petiolate** (e.g. mango) and without a petiole is called **sessile**. (e.g. *Calotropis*)
Usually it is solid and cylindrical structure but may be modified into different forms-

1. **Winged** - It becomes flat and leaf – like e.g. lemon, orange, etc (Fig. 3B).

2. **Spongy** - In some aquatic plants like water hyacinth, it becomes swollen and spongy, thereby providing buoyancy to the plant (Fig. 3C).

3. **Tendrillar** - It gets modified into tendril and helps the plant in climbing e.g. *Clematis*, *Nepenthes* (Fig. 3D)

4. **Phyllode** - It is modified into flattened leaf - like structure, e.g. Australian Acacia (Fig. 3E).

5. **Spiny** - In some plants like *Quisqualis* the leaf blade sometimes falls off and the petiole modifies into spine.

The Lamina or leaf blade (Epipodium)

Lamina is the most important part of the leaf. It is the seat of photosynthesis, transpiration and gaseous exchange. Usually it is a flat structure consisting of two surfaces. Upper surface which
faces the stem is called **adaxial or ventral** surface and the lower surface which is far from the axis is called **abaxial or dorsal** surface. The leaf is called dorsiventral when both the surfaces are different in structure, and isobilateral when both the surfaces are same.

**Shape of lamina**

The lamina shape may be -

i. **Acicular** - Needle shaped as in *Pinus* (Fig. 4A).

ii. **Linear** - Long, narrow and flat as in many grasses, wheat, etc. (Fig. 4B).

iii. **Lanceolate** - Lance shaped, wider at middle and narrower at base and apex as in *Nerium* (Fig. 4C).

iv. **Oblong** - More or less rectangular as in *Musa* (Fig. 4D).

v. **Subulate** - Tapering gradually from base to apex as in *Salsola* (Fig. 4E).

vi. **Ovate** - Egg shaped as in china rose (Fig. 4F).

vii. **Cordate** - Heart shaped with a deep notch at the base as in Piper beetle (Fig. 4G).

viii. **Sagitate** - The two basal lobes point towards the base and shaped like an arrow head as in *Sagittaria, Colocasia*, etc. (Fig. 4H)

ix. **Rotund** - Circular as in Lotus, Water lily, etc. (Fig. 4I).

x. **Hastate** - Like sagitate but the two basal lobes point outwards as in *Ipomoea* (Fig. 4J).

xi. **Obovate** - Wider at the apex and tapering gradually towards the base as in jack fruit (Fig. 4K).

xii. **Elliptical** - Wider at the middle like an ellipse as in *Vinca rosea*, guava, etc. (Fig. 4L).

xiii. **Spathulate** - Shaped like a spatula as in *Drocera* (Fig. 4M).

xiv. **Falcate** - As in *Eucalyptus* (Fig. 4N).

xv. **Oblique** - as in *Azadirachta* (Fig. 4O).

xvi. **Lyrate** - With a larger apical and smaller lateral lobes as in *Raphanus*, Mustard (Fig. 9P).

xvii. **Rhombate** - As in *Solanum* (Fig. 4Q).

xviii. **Runcinate** - Lamina with triangular apex and small lateral lobes towards lower sides as in *Sonchus* (Fig. 4R).

xix. **Cuneate** - Wedge shaped, wider at the apex and narrower at base as in *Pistia* (Fig. 4S).

xx. **Reniform** - Kidney shaped as in *Centella* (Fig. 4T).

xxi. **Lunate** - Shaped like a half moon as in *Passiflora* (Fig. 4U).

xxii. **Obcordate** - Reverse of cordate with a deep apical notch as in *Bauhinia* (Fig. 4V).
Fig. 4: Shapes of leaf lamina
A - Acicular, B - Linear, C - Lanceolate, D - Oblong, E - Subulate, F - Ovate, G - Cordate
H - Sagitate, I - Rotund, J - Hastate, K - Obovate, L - Elliptical, M - Spathulate, N - Falcate, O - Oblique
P - Lyrate, Q - Rhombate, R - Runcinate, S - Cuneate, T - Reniform, U - Lunate, V - Obcordate  Leaf margin
The margin of the lamina may be -

(i) **Entire** - Smooth as in mango (Fig. 5A).
(ii) **Repand** - Wavy as in *Polyalthia* (Fig. 5B).
   (iii) **Serrate** - Margins with large saw-like teeth pointed upwardly as in china rose, rose, etc. (Fig. 5C).
(iv) **Biserrate** - When teeth or margins are again serrated as in elm tree.
(v) **Dentate** - Margins with outwardly pointed teeth as in water lily (Fig. 5D).
(vi) **Crenate** - Margins with rounded teeth as in *Bryophyllum* (Fig. 5E).
(vii) **Spiny** - The marginal teeth are with spines as in *Argemone* (Fig. 5F).
(viii) **Lobed** - The margin is dissected to form lobes as in *Solanum* (Fig. 5G).

![Fig. 5 : Leaf Margins](image)

A - Entire, B - Wavy, C - Serrate,
D - Dentate, E - Crenate, F - Spiny, G - Lobed

**Leaf apex**

The apex of the lamina may be -

(i) **Acute** - Pointed and narrow as in mango (Fig. 6A).
(ii) **Obtuse** - The apex is broad, round and blunt as in banyan (Fig. 6B).
(iii) **Mucronate** - The apex is broad and round with pointed tip (Fig. 6C).
(iv) **Acuminate** - The apex forms a long tapering tail as in *Ficus religiosa* (Fig. 6D).
(v) **Emarginate** - A broad apex with a deep apical notch as in *Bauhinia* (Fig. 6E).
(vi) **Tendrillar** - The apex forms a tendril as in *Gloriosa* (Fig. 6F).
(vii) **Cirrhose** - The tip of broad apex forms a soft thread-like structure as in banana (Fig. 6G).
(viii) **Retuse** - A broad apex with an apical notch as in *Pistia* (Fig. 6H).

(ix) **Truncate** - When the apex is abruptly cut across as in *Paris polyphylla* (Fig. 6I).

(x) **Cuspidate or spiny** - The apex becomes hard and pointed like a spine e.g. date palm, *Pandanus* etc.

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![Fig. 6: Shape of leaf apices](image)

**Fig. 6: Shape of leaf apices**

A - Acute, B - Obtuse, C - Mucronate, D - Acuminate, E - Emarginate

F - Tendrilar, G - Cirrhose, H - Retuse, I - Truncate, J - Cuspidate

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**Venation**

The vascular system supplying a leaf reaches the base of the lamina and ramifies to give rise to one or more principal or main veins and their branches, the veinlets. The arrangement of veins and veinlets in a leaf is called venation. The conducting and mechanical tissues of the vascular system serve as a circulatory system as well as like a skeleton of the leaf. The arrangement of veins may be reticulate or parallel.

**Reticulate Venation**

This is the type of venation commonly found in dicotyledons. It may be of two types –

(i) **Unicostate reticulate or pinnate** – The main vascular supply forms *principal vein* or *mid rib* or *prominent costa* that gives of many lateral veins. Each vein divides repeatedly forming a reticulum e.g. Peepal, mango etc. (Fig. 7A).

(ii) **Multicostate reticulate or palmate** – The vascular supply after reaching the base of the lamina divides into two or more equally strong branches or costas. Thus there is no midrib and the branches spread out like fingers spread out from a palm of hand. It may be of two types-
(a) **Divergent** – When the costas spread out towards the margins of lamina and never meet as in *Cucurbita* (Fig. 7B).

(b) **Convergent** – When many costas, arising from the tip of the petiole, spread out in a curved manner and converge towards the apex of lamina as in *Zyzyphus* (Fig. 7C).

**Parallel Venation**

In this type veins run parallel to each other. It is found in monocotyledonous leaves. It may be **unicostate** or **multicostate** -

(i) **Unicostate** or **pinnate** – There is a principal vein from which many lateral veins arise and proceed in a parallel manner as in Banana (Fig. 7D).

(ii) **Multicostate** or **palmate** – Many principal veins arise from the tip of the petiole and proceed in a parallel manner. It may be –

(a) **Multicostate divergent** – Veins arising from the petiole diverge towards the margin of the lamina as in fan palms (Fig. 7E).

(b) **Multicostate convergent** – Parallel veins converge towards the apex as in Bamboo (Fig. 7F).
Types of leaves based on lamina dissection

1. **Simple leaf** -

   The ordinary leaves having one leaf blade are called simple leaves. Their margins may be entire or incised but incisions do not reach upto the midrib, e.g. mango, peepal, etc.

2. **Compound leaf**

   The lamina is incised upto the midrib or petiole, thus dividing it into many leaflets. The pattern of leaf dissection depends on the type of venation. There are two types of compound leaves -

   (i) **Pinnate compound leaves** - These leaves develop when incisions reach upto the midrib of leaves having unicostate reticulate venation. The midrib is now known as **rachis** and the leaflets are arranged along two sides of the rachis. Pinnate compound leaves may be -

      (a) **Unipinnate** - Leaflets are borne on both sides of the rachis. It may be -
**Paripinnate** - Leaflets are borne in even number or in pairs as in Tamarind (Fig. 8A).

**Imparipinnate** - Leaflets are borne in odd number and the rachis is terminated by a leaflet as in rose (Fig. 8B).

(b) **Bipinnate** - Leaflets or pinnae of first order divide again into pinnules as in *Acacia, Albizia*, etc. (Fig. 8C)

(c) **Tripinnate** - Pinnules of bipinnate leaf are dissected again to form tertiary pinnules as in *Moringa* (Fig. 8D).

(d) **Multipinnate or dicompound** - When incision of lamina occurs more than three times as in coriander, fennel, etc. (Fig. 8E).

(ii) **Palmate compound leaves** - Such leaves develop from palmate leaves with multicostate venation. Incisions extend up to petiole and the leaf blade is dissected into many leaflets. All leaflets are attached to the tip of petiole and appear to be radiating like fingers from a palm. Palmate compound leaf may be -

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*Fig. 8: Diagrams showing different types of compound leaves. A to E Pinnately compound leaves: A - Paripinnate, B - Imparipinnate, C - Bipinnate, D - Tripinnate, E - Multipinnate. F to J - Palmately compound leaves: F - Unifoliolate, G - Bifoliolate, H - Trifoliolate, I - Quadrifoliolate, J - Multifoliolate.*
(a) **Unifoliate** - A single leaflet is articulated to the petiole as in lemon, orange, etc. (Fig. 8F).

(b) **Bifoliate** - Number of leaflets is two as in *Hardwickia bipinnata* (Fig. 8G).

(c) **Trifoliate** - Three leaflets are articulated as in *Aegle marmelos, Oxalis corniculata*, etc. (Fig. 8H)

(d) **Quadrifoliate** - When leaflets are four as in *Paris quadrifolia* (Fig. 8I).

(e) **Multifoliate** - When number of leaflets is more than four as in silk cotton (Fig. 8J).

**Modifications of Leaves**

In some plants leaves modify to carry out some specific functions.

1. **Leaf tendril** - Entire leaf (in *Lathyrus odoratus*, Fig. 9A), upper leaflets (in *Pisum sativum*, Fig. 9B), terminal leaflet (in *Narvelia*, Fig. 9C), leaf tip (in *Gloriosa*, Fig. 9D), petiole (in *Clematis*) or stipule (in *Smilax*), modify into thin, soft wiry structure known as tendril. Tendrils coil around the support and help the plant in climbing.

2. **Spines** - As in *Opuntia* (Fig. 9E, F).

3. **Hooks** - Upper three leaflets modify into hooks as in *Bigonia* (Fig. 9G).

4. **Scales** - Leaf modify into a thin, dry, membranous structure as in *Ruscus*.

5. **Phyllode** - Petiole forms a leaf-like structure as in Australian Acacia (Fig. 3D).

6. **Insectivorous plants** - In *Nepenthes* the lamina modifies into pitcher and the leaf apex into its lid (Fig. 9H). Petiole forms tendril and leaf base becomes flat. In *Utricularia* (bladder wort) whole leaf modifies into a bladder (Fig. 9J). In *Droceria* tentacles are found on the leaf-blade (Fig. 9I). The tentacles secrete sticky fluid in which insects are entangled. In *Dionoea* the midrib acts as a hinge and as soon as an insect touches the leaf, it is trapped.

7. **Fleshy leaf** - Leaves of some plants store food and water and become fleshy as in *Aloe*. 
Fig. 9: Modifications of leaves
(A-D) Leaf tendrils; A - Entire leaf, B - Upper leaflets, C - Terminal leaflet, D - Leaf tip modified into tendril
(E-F) Leaf spines; (G) Hooks; (H-J) Leaf modified into insect catching structures; H - Nepenthes, I - Drosera, J - Utricularia
Arrangement of leaves –

At each node two or more leaves may be found. The arrangement of the leaves on stem or branch is known as phyllotaxy or phyllotaxis. Three principal types of arrangements are found in plants -

**Whorled**: When at each node more than two leaves occur in the form of a whorl or cycle (Fig. 10D) e.g. *Nerium*.

**Opposite**: When each node bears two leaves placed opposite to each other. It may of two types –

(i) **Opposite decussate** – Here the pairs of opposite leaves at successive nodes lie at right angles to each other as in madar (*Calotropis*) (Fig. 10B).

(ii) **Opposite superposed** – In this condition the pairs of opposite leaves of successive nodes lie one above the other (Fig. 10C). This is seen in *Quisqualis*.

![Phyllotaxy Diagrams](image)

Fig. 10: Phyllotaxy (A) Alternate spiral (B) Opposite deussate (C) Opposite superposed (D) Whorled (E) Leaf mosaic
Alternate or spiral: When a single leaf arises at each node and the leaves are arranged spirally on the stem (Fig. 10A). Now if an imaginary line is drawn touching the bases of successive leaves, it will form a spiral on the stem (Fig. 11A). This spiral is called the genetic spiral. The genetic spiral can be drawn in a flat surface to form a flat spiral on which the position of leaves may be marked (Fig. 11B). The straight vertical line along which the leaves are arranged is termed orthostichy. The angle between the two consecutive leaves is called the angular divergence.

Leaf mosaic

When stalks of leaves are of unequal length so that the leaves do not cover each other and all the leaves are brought to the same level (Fig. 10E) e.g. Oxalis.

Origin, differentiation and development of the foliage leaf

The different leaf forms are, in general, a consequence of differential activities of the various meristems involved in leaf development. About five different types of leaf meristems are responsible for the overall development of a leaf. These are: apical, intercalary, marginal, adaxial and plate meristems. These may function one by one in the above sequence or two or more of them might working simultaneously.

The process of formation of the leaf can be divided into the following stages: origin from shoot apical meristem, early differentiation, development of the leaf axis, origin and differentiation of the tissues of the lamina and development of the veins.

1. **Origin from shoot apical meristem** - The leaf is initiated with divisions in a small group of cells on the sides of the shoot apex. In angiosperms, there is no uniformity in the site of division. For example, in grasses the main portion of the leaf primordium originates from the outermost cell layer of the shoot apex whereas in some other monocotyledons and majority of dicotyledons the first periclinal division takes place in the cells of one or more layers below it. Most commonly initiation of the leaf primordium commences with
periclinal divisions in cells of the subsurface layer or the corpus. These divisions are accompanied by anticlinal divisions in the surface layer or the tunica. The initial periclinals are also followed by further divisions of adjacent and underlying cells, resulting eventually in elevation of the leaf primordium above the surface of the shoot apical meristem.

There has been a search for the genes whose expression correlates with particular features of functioning of apical meristem such as the initiation of leaf primordia. Some recent studies like those on shoot apices of Arabidopsis, maize etc. have revealed some interesting clues indicating the possible gene expression in apical meristems. The knotted 1 gene in maize and knotted 1 - like gene in Arabidopsis are such examples. These two genes show similar expression in different parts of the shoot apex. In maize the knotted 1 gene is expressed in corpus and not in the peripheral zone whereas in Arabidopsis the knotted 1 - like gene is expressed in the peripheral zone and not in the central zone of the shoot apex. The cells with similar genetic constitution show different gene expression but all cells are in constant communication with one another. The cells communicate to coordinate their activities in response to changing conditions such as dark, light, temperature, etc. which direct the growth of leaves, branches, flowering and fruiting etc. Very less is known about intracellular signaling mechanisms involved in the cell communications in plants. Out of the various signalling pathways suggested, cell surface receptor kinases (e.g. CLAVATA in Arabidopsis) are said to be used in cell to cell communications.

2. **Early differentiation** - As a result of continued cell division in cells of surface and subsurface layers, the leaf primordium protrudes from the shoot apex as a leaf buttress. As soon as the foliar buttress is formed, certain cells at its centre now divide actively and a small finger-like protuberance emerges out from the buttress. This protuberance actually is the axis of the young leaf. It proceeds to grow in size for some time by the activity of the apical meristematic cells (i.e. the leaf apical meristem). Soon the protuberance grows laterally. It consists of a protoderm and a procambial strand.

3. **Development of the leaf axis** - In many dicotyledons, development of the lamina or lateral leaflet is preceded by the early differentiation of leaf axis. After a particular height, the leaf apex begins to show evidences of histological maturation and all further increase in length is due to the cell division and cell elongation in the region distal to the tip, i.e. by the intercalary meristem.

4. **Origin and differentiation of tissues of the lamina** - A strip of cells beneath the protoderm called adaxial meristem is often responsible for an increase in thickness of the leaf axis. The lamina is initiated in the early stages of elongation of the leaf axis from two wing-like strips (Fig. 12) or bands of meristematic cells located along two margins of the leaf axis. These meristematic cells constitute the marginal meristems. The two meristematic bands are turned inwardly, i.e. toward the adaxial side of the leaf, so that the lamina develops towards the apical meristem and eventually encloses it. Each marginal meristem consists of a row of marginal initials, a row of submarginal initials and the immediate derivatives of these initials.
The middle cell layers on the adaxial side may show some periclines so that width of this region is increased. These meristematic cells constitute the adaxial meristem and are responsible for growth in thickness. The marginal initials or surface initials divide anticlinally to produce the protoderm. The submarginal or subsurface initials produce mesophyll and the vascular bundles. These initials divide alternately by anticlinal and periclinal divisions. Anticlinal divisions result in the formation of adaxial and abaxial layers of mesophyll whereas the periclinal results in the formation of middle layers. After the formation of all layers the cells divide only anticlinally thus exhibiting an increase in surface area but not in thickness of the leaf. Each cell divides to give a small plate of cells and the whole lamina functions as a plate meristem, i.e. the meristematic cells arranged in parallel layers dividing only anticlinally to constitute plate meristem. By the activity of plate meristem the leaf attains its final size.

Fig. 12: Diagram showing developmental stages of a foliage leaf
A&B - L.S. and T.S. of Young leaf;
C - L.S. at later stage
The regular arrangement of cell layers is interrupted by the development of the vascular bundles. As a result of differential enlargement and division of cells the different parts of the leaf expand at different rates and in different directions. An anticlinal elongation accompanied by anticlinal divisions result in formation of palisade. The cells forming spongy parenchyma also divide anticlinally, but less frequently than the palisade cells and usually they remain isodiametric in shape.

5. Development of the veins - In dicotyledonous leaves, the procambium of the midvein differentiates in the leaf axis during early stages of lamina development. With the commencement of the development of the lamina procambial strands differentiate in its middle layers giving rise to the large lateral veins, then to the successively smaller veins.
The procambial strands of small veins develop basipetally during the intercalary growth of the lamina.

The procambium of the midvein differentiates acropetally (i.e. in upward direction), the lateral veins of the first order develop from the midrib toward the margins and the small veins differentiate basipetally. The differentiation of vascular tissues of leaf begins before its procambial system is completely differentiated. The protoxylem differentiates first, followed by the protophloem and both differentiate acropetally. After the final elongation of the veins metaphloem and metaxylem differentiate basipetally in the larger strands in which the differentiation of the protophloem and protoxylem is completed, and then in the smaller basipetally differentiating strands where there is no protophloem and no protoxylem.

A compound leaf is also initiated just like a simple leaf axis upon a buttress. The leaflets arise as margins of the buttress as protuberances and resemble the marginal growth of a simple leaf. Histogenesis and later developmental stages of a leaflet also resemble those of a simple leaf.

As has been discussed above through activities of different leaf meristems and a well defined program of cell proliferation and cell enlargement, each leaf primordium and its adjacent cells will grow to form a leaf, a node and an internode. Meanwhile, the apical meristem itself will give rise to new leaf primordia, so as to generate more and more modules (leaf + node + internode) in a potentially unending succession. The youngest primordium is of course nearest the apex and as the apex grows on and age of primordium is increased, its typical leaf form is developed. The ultimate size and shape of leaf, however, will be determined by a number of factors such as size of primordium, rate of cell division and cell enlargement, duration of the growing season, etc. There is a system of local signals within the apical meristem region which determines the pattern of primordia - the location of new primordium in relation to the shoot apical meristem, its position relative to the next primordium and the spacing between the two primordia.

Axillary bud primordium is formed in the angle between leaf primordium and stem. These buds either remain quiescent (inactive / dormant) or may develop into a new branch or other structure such as flower. The axillary bud primordium is generally formed only when the leaf primordium is in its second or third plastochron stage and its fate is decided by its genes as well as the environmental conditions. As separate plant parts are faced to different environmental conditions and react to them individually by changes in their mode of development.
Internal structure of leaf in relation to photosynthesis and water loss

Internally the leaf consists of the dermal system, ground tissue system and the vascular tissue system.

**Epidermis**

The leaf is covered on both surfaces by epidermis. Compact arrangement of cells and presence of cuticle and stomata are the main features of the leaf epidermis. Thick and cutinized outer walls of epidermal cells do not rapidly allow the water to pass through them and thus reduces transpiration to a great extent.

Numerous stomata are found in between the epidermal cells. Each stoma is surrounded by two guard cells. These cells have specialized shape and structure. They are bean shaped in dicotyledons and dumb-bell shaped in grasses. They contain chloroplast. Their inner walls (towards the aperture) are thick and they can regulate opening and closing of stomata. The guard cells may remain surrounded by two or more subsidiary cells. In dorsiventral layers of dicotyledons, where the leaves are horizontally placed the stomata are confined to lower surface. They are very few in the upper epidermis and sometimes altogether absent. In isobilateral leaves of monocotyledons, where leaves are vertically placed, they occur in equal number on both the surfaces. In floating leaves they are confined only to the upper surface and in submerged leaves they are totally absent. The stomata may be on the same level as the other epidermal cells, or above the surface of the epidermis (raised stomata) or below it (sunken stomata) depending upon requirements.

The function of transpiration and gaseous exchange between the plant and the atmosphere is performed by the stomata. Each stoma opens into a substomatal chamber or respiratory cavity which facilitates the diffusion of gases properly.

**Mesophyll tissue**

The tissue of the leaf that lies between the upper and lower epidermis excepting the veins is known as mesophyll. It usually undergoes differentiation to form the photosynthetic tissues. In many plants, especially among the dicotyledons the mesophyll consists of two types of cells: palisade parenchyma and spongy parenchyma.
The palisade tissue consists of elongated and more or less cylindrical cells found below the epidermis and are arranged compactly in one or more layers. The palisade cells are arranged near to the upper (adaxial) surface of the leaf where they receive more sunlight and perform the function of photosynthesis. In some plants (e.g. *Thymelea*) the palisade parenchyma is found only on the lower (abaxial) side of the leaf. In certain plants (e.g. *Dianthus caryophyllus*), palisade parenchyma is present on both sides of the leaf. Leaves with palisade parenchyma on one side of the leaf and spongy parenchyma on the other are termed **dorsiventral** or **bifacial** (e.g. many dicots). Leaves which contain palisade parenchyma on both sides are said to be **isobilateral** or **isolateral** (e.g. many monocots).

The spongy parenchyma usually consists of loosely and irregularly arranged thin walled cells having large intercellular spaces (air spaces) among them. These cells contain lesser number of...
chloroplasts than palisade cells. Due to the presence of large air spaces, the spongy tissue is more adapted to the exchange of gases between the cells and the atmosphere.

**Vascular tissues**

In leaves with reticulate venation (most of the dicotyledons), the largest vein passes through the median part of the leaf and forms the main vein which gives rise to smaller veins. In leaves with parallel venation (most of the monocots), all veins may be of the same or different thickness. The veins of a leaf are continuous through the petiole with the vasculature of the stem. When we cut transverse section of a stem, the veins are seen in the form of vascular bundles.

The conducting tissues are situated near or at the centre of the midrib. This system may be in form of a ring, a crescent shaped ring or scattered patches. In the ring shaped conducting system, parenchyma cells are usually found in the centre of the ring, the xylem towards upper surface and the phloem towards lower surface. Xylem consists of vessels, trachieds, wood fibres, and wood parenchyma. Xylem conducts water and raw food materials to the leaf.

The phloem consists of sieve tubes, companion cells and phloem parenchyma. The phloem translocates the prepared food material from leaf to other parts of the plant. The large veins are structurally similar to that of a midrib. The small veins consist of a few conducting cells.

**Bundle sheath**

The small vascular bundles are usually surrounded by a layer of tightly packed parenchyma cells forming the bundle sheath. These cells may or may not have chloroplasts. In some plants (e.g. members of family Winteraceae) the bundle sheath is sclerenchymatous. Large vascular bundles generally possess bundle sheath extensions which extend as parenchymatous or sclerenchymatous mass both towards lower and upper epidermis.
In plants with the C4 pathway of photosynthesis (members of family gramineae, Euphorbiaceae etc.), bundles in leaves remain surrounded by radially oriented mesophyll cells. This type of leaf anatomy was called **Kranz type** by Haberlandt (1918). The chloroplasts of the bundle sheath of these plants accumulate starch and may differ in ultrastructure from the mesophyll chloroplasts.

**Dicotyledonous (dorsiventral) leaf** - In these leaves (e.g. Mango, Banyan, *Nerium* etc.) only upper surface is illuminated directly. The leaf is covered by an epidermis on either surfaces. There are very few (stomata) present in upper epidermis whereas abundant stomata are present in the lower epidermis. Cuticle is thicker on the upper surface than the lower. The palisade cells are arranged near to the upper surface. These cells possess abundant chloroplasts. The tissues extending from palisade to lower epidermis is the spongy tissue. Number of chloroplasts is much lesser here thus explaining the pale green colour of the lower surface of the leaf. Number and size of vascular bundles decrease gradually from base to apex. Vascular bundles are conjoint, collateral and closed. The protoxylem is situated towards upper epidermis and metaxylem towards lower epidermis. Phloem lies towards the lower epidermis.

**Monocotyledonous (Isobilateral) leaf** - Usually the leaves of monocotyledonous plants like wheat, maize, etc. receive equal amount of sunlight on both the surfaces. Stomata are equally distributed on both the surfaces and cuticle is also equally lesser thickened. Sometimes in upper epidermis (e.g. maize, grasses, etc.), larger colourless cells, the bulbiform cells are found. The mesophyll is not differentiated into palisade and spongy parenchyma. The vascular bundles are arranged in a parallel series and the bundles are conjoint, collateral and closed type.

**Leaf Adaptation to water loss stress**

The plants that grow in arid habitats develop structural characteristics and different mechanism to overcome water stress conditions. Through these mechanisms plants minimize the intensity of
the effect of stress (**stress avoidance**) or they develop in-built capacity in them to face the situation (**stress tolerance**).

Some plants avoid the stress by completing their life cycle before the onset of unfavourable environmental conditions (**water savers**) whereas some other plants achieve this either by reducing transpiration or by increased water uptake (**water spenders**). The plants that grow in arid habitats and whose transpiration decreases to a minimum under conditions of water deficiency are called **xerophytes** (Maximov, 1931). Such plants are also termed xeromorphic plants. They can withstand a prolonged period of drought and remain uninjured. For this purpose they have certain peculiar adaptations. The characteristic anatomical features of the xerophytes are -

**Epidermis and cuticle** - Heavy cuticularization and extreme cutinization of the epidermis and even of sub-epidermal cells are common in xerophytes. In extreme xerophytes along with well developed cutinized layers the epidermal and subepidermal cells also become lignified. In *Calotropis* and some other plants, a covering of wax is formed on the epidermis. In the leaves of *Nerium* and *Ficus*, the epidermis becomes multilayered.

**Hypodermis** - Many xerophytic plants possess single or multilayered hypodermis with cutinized or lignified cells. The mucilage, gums and tannins are commonly in this present layer.

**Stomata** - The xerophytes generally possess less number of stomata. In some plants the leaf surface is reduced thus reducing the number of stomata. Usually the stomata are present in pits or depressions. Such stomata are commonly known as **sunken stomata** (e.g. *Hakea*, *Agave*, *Nerium*, etc.). These depressions may contain hairs which protect the stomata from direct attack of wind gusts (Fig. 18, 19).

**Sclerenchyma** - Xerophytes commonly have a large proportion of sclerenchyma. The sclerenchyma prevents transpiration to some extent. It also provides mechanical strength to the plant body (e.g. *Banksia*, *Dasylirion* etc.)

**Hairs** - Mostly hairs are confined to the lower surface of leaf. Hairs cover the stomata thus preventing rapid evaporation of water. Plants possessing abundant hairs on their surface are termed as **trichophyllous**.

**Rolling of Leaves** - In many xerophytic grasses, the stomata are confined to ventral surface only. In these plants, special motor cells (hinge) are present on the upper surface which cause inward rolling of leaves under dry conditions (e.g. *Amonophila arenaria*). As the leaves roll up, the stomata occupy a hidden position on the inner surface thus minimizing the rate of transpiration.
Reduced leaf surface - In many xerophytes reduced needle-like or scaly leaves are found. This way, reduction in total exposed surface takes place reducing thereby the rate of transpiration (e.g. *Casuarina, Asparagus* etc.)

Water storage tissue - In many xerophytes, special parenchymatous tissue is used for storage of water (e.g. *Aloe* etc.). In rainy season, water is quickly absorbed and stored and then used slowly during the period of drought.
Abundant palisade - In leaves of xerophytes, the palisade is compact and found in abundance. In some plants (Nerium) it occurs near both the surfaces.

Latex tubes - In many xerophytic plants laticiferous canals are found (e.g. Calotropis, Euphorbia etc.). Viscosity of latex reduces the rate of transpiration to some extent.

Vascular System - It is very well developed.

Senescence

Senescence is the final phase of development leading to cellular breakdown and death. It occurs when catabolic processes exceed metabolic ones. It is an energy dependent development process which is controlled by plants own genetic system. Senescence can be observed at different levels. These are -

1. **Molecular level** - Enzymes, nucleic acids, chlorophyll, etc. are important biochemical substances which are present in the cells. Degradation of these substances is a continuous process. As the process of degradation occurs, they are constantly being replaced by their new synthesis in the cell.
2. **Organelle level** - Nearly all cell organelles (mitochondria, chloroplasts, lysosomes, etc.) show senescence. The degradation and resynthesis of organelles and other substances is collectively termed as turn over.

3. **Cellular level** - Individual cells also show senescence, e.g. differentiation of a sclereid, formation of cortic cells, tracheid, vessel elements, etc.

4. **Organ level** - Shedding of cotyledonary leaves, periodic falling of leaves, flowers, fruits etc. are some examples of senescence at organ level.

5. **Organism level** - Many plants (e.g. rice, wheat, gram, etc.) die soon after production of seeds.

During senescence, many cellular proteins, carbohydrates nucleic acids, etc. are broken down by hydrolytic enzymes. The components obtained after hydrolysis and many other minerals are transported out of senescing organs. These are transported back into the main body of the plant by phloem.

The leaves are periodically detached from the perennial plants. In deciduous trees all the leaves senesce and die at the same time. This type of senescence is called **synchronous** or **simultaneous senescence** and is believed to be controlled by environmental factors. The level of endogenous hormones like auxins, gibberellins etc. is more during long days and low during short days. It is believed that the decreased level of these hormones during short days causes falling of leaves. The advantage of synchronous leaf fall is that the plant escapes transpiration under unfavourable condition. By falling of leaves, recycling of nutrients takes place and they are thrown back into the soil.

**Sequence of leaf senescence**

Senescence of leaves is associated with following changes -

- Breakdown of chlorophyll results in the yellowing of leaves.
- Membrane of grana is broken down.
- Endoplasmic reticulum degenerates and ribosomes disappear gradually.
- Mitochondria are degenerated.
- The RNA content decreases gradually.
- Protein content decreases due to activity of proteolytic enzymes.
- Amino acids are exported out of the leaves to other parts of the plant like young leaves, seeds, fruits, etc.
- Loss of rubisco activity.
- Rate of respiration is decreased.

**Molecular mechanism of senescence**

During senescence some organelles are destroyed while others remain active. The first organelle to be deteriorated is chloroplast whereas the nucleus remains intact until the later stages of senescence. During senescence, synthesis of various hydrolytic (proteases, nucleases, lipases) and chlorophyll degrading enzymes takes place. Synthesis of these enzymes involves the activation of specific genes.
Decrease in level of most leaf mRNAs is noticed during senescence, but level of certain specific mRNA transcripts has been found to be increased. Such genes whose expression decreases during senescence are called **senescence down regulated genes** (SDGs). SDGs include genes encoding for proteins involved in photosynthesis.

Genes whose expression is induced during senescence are called **senescence associated genes** (SAGs). SAGs include genes encoding for hydrolytic enzymes as well as enzymes involved in the biosynthesis of ethylene (e.g. ACC synthetase, ACC oxidase). Another class of SAGs encode for enzymes involved in the conversion or remobilization of breakdown products.

**Factors affecting senescence**

Following factors affect senescence -

1. **Nutrients** - Deficiency of some nutrients, such as nitrogen, promote leaf senescence. Exogenous supply of nitrogen can delay this senescence for some time. Nitrogen is known to increase the level of cytokinins and that delays the process of senescence.

2. **Water supply** - Increased level of abscissic acid (ABA) is known to accelerate the process of senescence.

3. **Light and darkness** - Senescence is faster in darkness than in light. This may be because of slower degradation of chlorophyll in light than in dark. Stomata also remain closed during dark causing accumulation of ABA inside the leaves.

4. **Temperature** - At high temperature, degradation of chlorophyll and protein increases thus increasing the rate of senescence. Senescence is delayed at low temperature.

5. **Hormones** - Cytokinins delay senescence. Cytokinins such as zeatin riboside and dihydrozeatin riboside are involved in delaying senescence.

Ethylene on the other hand enhances the rate of leaf senescence. Treating leaves with ACC (a precursor of ethylene) or ethylene accelerates their senescence. Enhanced ethylene production causes loss of chlorophyll which is a characteristic feature of leaf senescence. Substances that inhibit the synthesis of ethylene retard leaf senescence. ABA is also known to accelerate senescence. It enhances the breakdown of proteins and nucleic acids by stimulating several hydrolases.

**Significance of senescence**

1. If the causes of senescence are known it can be delayed and thus the age of plant organ or whole plant can be increased.

2. During senescence, the component sugars, nucleosides, minerals, amino acids are transported back into the main plant body and reutilized in development of new leaves and buds.

3. The deciduous trees can tide over the adverse environmental conditions by senescence of their leaves.
Abscission

Periodic defoliation is a notable feature of the perennial trees. The deciduous plants shed their leaves at the approach of winter. The evergreen plants may shed their leaves in any season. Some structural modifications occur in a particular region at the base of the leaves and finally they are abscissed. This particular region is known as **abscission zone**. The formation of this zone is initiated before the leaf fall. The leaves now turn yellowish in colour due to disintegration of chlorophyll and enhancement of carotenoid pigments. The waste products are transferred to the leaves, so that they are also removed from the plant with the leaf fall. These changes take place in living cells at the base of the petiole. The leaves of the dead branches are not shed, but they dry up and decay in course of time.

The abscission zone is a narrow zone composed of two parts, an abscission layer or separation layer and a protective layer. Externally it appears as a groove or construction around the base of the petiole in simple leaves. It is visible at the base of rachis as well as at the base of individual leaflets in compound leaves. In sessile leaves this zone may be the only remnant of the petiole.

![Diagram of abscission zone](image)

**Fig. 20**: Abscission of leaf (A) A petiole showing abscission zone and protective layer (B) Magnified view of petiole

Histologically the **separation layer** may be recognized as a plate of cells oriented transversely across the petiole. Generally cells in this area are smaller and thinner walled having denser protoplasm and abundant starch grains. The vascular bundles in this region become reduced and have trachieds and weakly developed sclerenchyma. Vessels are usually lacking in them. Sometimes there may be clogging of tracheary elements by gums and tyloses and deposition or callose in sieve elements below the zone. The process of abscission involves enzymatic degradation of cell walls. The middle lamella and the outer walls of the parenchyma cells swell up, become gelatinous and eventually break down. The cellulose walls are hydrolysed. The calcium pectate present in the middle lamella converts into water soluble pectin. At the end, the cells become quite separate and free from each other. Now the leaf remains attached to the stem by the vascular elements only which break down very soon by wind or by the weight of the leaf.
itself separating the leaf from the stem. This process becomes quicker during rains due to hydrolysis of gelatinous cell walls and increased weight of the leaf. The formation of separation layer is very significant. If a leaf dies or break off without formation of a separation layer, the stem tissue may be exposed to various infections or extensive tearing may take place. So separation layer functions as a point of rupture and ensures the abscission of leaf without loss.

The **protective layer** is formed just proximal to the separation layer shortly after the leaf fall and consists of a group of cells that divide and form sealing layer or cover to the scar caused by leaf fall. The protective layer may be of primary type if it is formed as a result of the lignification and suberization of the parenchyma cells in this region or the cells arising from them by divisions. It is called secondary if it is formed by a cork cambium developing on the inner side which eventually forms a periderm which becomes continuous with the periderm of the stem.

**The Root System**

Roots of higher land plants anchor the body in the soil and absorb water and nutrients. However, in submerged or floating hydrophytes anchorage to soil or absorption of water is not done by roots, so, in these plants roots are lesser developed or absent.

The root and the stem constitute a continuous structure and have common features in form, anatomy, function and method of growth. However, basic differences in the development and arrangement of the primary tissues in these two organs are always distinguishable.

Roots constitute the lower part of the plant axis which is nongreen and typically grows towards gravity. Roots are positively hydrotropic and negatively phototropic. These are the first organs of the plant which start growing as seed germinates. They do not possess nodes and internodes. Roots are also branched but they bear only similar type of branches as against stem where dissimilar branches - flowers, leaves, vegetative branches - are present. Roots do not have axillary buds. The lateral roots arise endogenously from the pericycle. Their tips or growing points are covered by a special structure, the **root cap**, which is absent in stems.

Roots are much more variable in shape and structure primarily because of number of obstructions and moisture contents of the soil. But in many cases other environmental and functional aspects are related to these variabilities.

The main root which is a direct prolongation of the radicle is called the **tap root**. Branches on the tap root are called as secondary roots and those on secondary roots as tertiary roots and so on. The main root alongwith branches of various orders constitute, the **tap root system** or normal **root system**, e.g. root system of most dicotyledons. The main root in this system is well developed and stout and thicker than the lateral branches. These roots are also called **deep feeders** as they remify through a very large and deep area in the soil. Their branching pattern is generally called racemose type. The order of formation of the lateral roots is from the root neck, i.e. the part where the root joins with the stem, towards the root tip. Such roots are generally present in trees. In some annual herbs the tap root does not grow very deep and the secondary branches grow deeper and spread horizontally. These roots are said to be branched in cymose pattern.

In most of monocotyledons the **adventitious root system** is found. In this type the new roots grow from near the base of the radicle. These grow and behave in the same manner as the normal primary root system. These are called **seminal roots**. Later on more roots arise from the basal
nodes of the stem. These are called **fibrous roots**. As these roots to not grow very deep, they are also known as **surface seeders**, e.g. grasses.

Whether a root belongs to tap root or adventitious type, it constitutes five main regions or zones. These are the rootcap zone, the meristematic zone, the root elongation zone, the root hair zone and the mature root.

![Diagram of root regions](image)

**Fig. 21: Diagrammatic sketch of a typical root showing different regions**

**The rootcap region**

It is a characteristic region found in roots only and occupies the terminal position. It is a small cap-like structure which protects the delicate growing point of root when it grows down in the soil. In most of the plants, where present, it is a simple structure. Variations are found in certain plants. For example a multiple root cap is found in *Pandanus*, and is replaced by sac-like structures called **root pockets** in aquatic plants like *Eichornia, Lemna, Pistia* etc. The root pockets are loose thimble – like structures covering the root apex. Root pockets also differ from the root cap in that they do not regenerate whereas in terrestrial plants the root cap is continuously renewed as its outer layers are gradually sloughed off due to friction with soil particles.

**The meristematic region**

It is the sub-distal region of the root constituting small, densely stained, isodiametric cells which are compactly arranged. Depending upon the arrangement, behaviour and function, etc. of this region, various theories of apical organization have been proposed.

**The cell elongation region**

Proximal to the meristematic zone, the cells show elongation resulting in pushing the root tip deep into the soil. Cells in this region absorb minerals from the soil.
The cell maturation region

Cells of this zone undergo differentiation so that different mature permanent tissues are formed which are organised into the typical tissue systems of the root viz., epidermis, cortex, vascular tissue system etc. The unicellular root hairs, which are characteristic feature of the roots, developed in this region, are mainly responsible for water absorption. As the root grows, the older root hairs become nonfunctional and the function of water absorption is continued by the newly formed root hairs.

The mature region

Well differentiated permanent tissues are present in this region. Further, this region is characterized by an abundance of root hairs. Secondary growth and origin of lateral roots are the other characteristic features of this region.

Structural modifications of roots

To carry out some special physiological or mechanical functions, roots may undergo modifications. Some important modifications are as follows -

Modifications for storage of food

In some plants tap roots or adventitious roots become fleshy by storing extra food. Mostly these roots are named according to the shapes assumed by them. Roots swollen in the middle and gradually tapering towards both the ends are named as fusiforms e.g. radish (Raphanus sativus). It is conical, when broadest as top and gradually taper towards the lower end e.g. carrot (Daucus carota). Napiform root is much swollen above and abruptly tapers towards the lower end, e.g. beet (Beta vulgaris). In some plants roots originate from the nodes of the running stems. These become swollen and form the edible root tubers as in sweet potato (Ipomoea batata). If adventitious roots swell up and form clusters they are known as fasciculated roots (Asparagus). Roots having alternately swollen and constricted parts forming a beaded structure are called moniliform or beaded roots (Portulaca and Momordica). If the tip of root becomes swollen like one bead it is called nodulose (e.g. Curcuma amada). Annulated roots look like as if formed by a number of discs placed one above the other (e.g. Psychotria).
Modifications for respiration

The soil near sea shores is highly saline and devoid of oxygen. At these places, some trees and shrubs (e.g. mangrove plants) develop negatively geotropic roots. These roots grow vertically up into the air and are called **penumatophores** or **respiratory** roots. Minute pores or special lenticels (pneumathodes) are found on these roots, through which air enters into the roots. Common examples of plants having respiratory roots are *Heritiera, Rhizophora*, etc.
Modifications for reproduction

Roots of some plants develop adventitious buds which separate and form new plants (e.g. Ipomoea batata). New plants arise from the basal part of many garden plants in this way. Root cuttings are the main mode of reproduction in many plants like Trichosanthes dioica. Members of family Podostemaceae propagate through roots. Thus, those roots which help in reproduction are called reproductive roots.

Fig. 23: Respiratory roots

Fig. 24: Tuberous root of sweet potato with developing adventitious buds
Modifications for interaction with microbes

Roots of some plants (e.g. mycorrhizal saprophytes) are infested with some fungal mycelia. These mycelia form a mantle-like structure on the root which absorbs soluble food. This food is utilised by both the host plant and the fungus. These roots become abnormal in shape and show stunted grow. Root hair do not develop on them and their tips do not grow. These mycorrhizal roots are found in saprophytes like Monotropa and trees like pine and birch.

Fig. 25: (A) A mycorrhizal root of pine (B) Schematic diagram showing growth of mycorrhizal fungus within the tissues of the root
Many plants like members of family leguminosae develop root nodules due to infection of bacteria. These roots secrete some growth factors (IAA) or chemical substances in the surroundings which help in multiplying the bacteria very fast near the roots. These bacteria penetrate the root hair tip or invade through damaged or broken root hair.

A tubular infection thread develops in the root hair cell through which the bacteria enter into the root hair. The infection thread containing bacteria grows fast and from root hair cells reaches to pericycle passing through the cortical parenchyma and endodermis. Cells of endodermis and pericycle divide rapidly and an outgrowth comes out in the form of knob-like nodule at the surface of the root. A large number of knob-like protuberances or nodules can be seen on the roots of these plants. The bacteria inducing the formation of nodules are able to absorb atmospheric nitrogen and by the process of N\textsubscript{2} fixation change it into various nitrogen compounds suitable for absorption. In return, these bacteria receive carbohydrates from the roots of the plants.

![Diagram of root system showing nodules](image)

**Fig. 26 : (A) Root system of Soybean showing nodules  
(B) A part of root showing process of infection**

**The root apical meristem**

The concept of meristems brings out the importance of the apical meristems in relation to the building up of the plant body. Early investigations on apical meristems revealed a pre-occupation with analysing the cell patterns at the apices and typifying them. Attempts at interpreting different patterns observed in the apical meristems gave birth to a number of theories or concepts. Some of these were put forward with particular reference to root apices.

Nägeli (1844) during his studies on algae, mosses and ferns observed a single tetrahedral apical cell at the shoot apex and at the root apex. A careful study of longitudinal sections revealed the derivation of all cells of the plant from this apical cell. It was observed that such an apical cell is present at the root and shoot apices of most of the vascular cryptogams. It was also supposed that a single initial cell of this kind would be found in apices of all higher plants also and the theory led to extensive investigations which ultimately proved unsuccessful in higher plants and the apical cell theory was superseded by the histogen theory.

The histogen theory was put forward by Hanstein in 1868 particularly to interpret the cellular pattern at the shoot and root apices of higher plants. According to Hanstein's proposition there
are three superimposed and independent tiers of initials, called **histogens**, present in the apical meristems. The three histogens were named as **dermatogen**, **periblem** and **plerome** which gave rise to the epidermis, cortex and central cylinder respectively. The histogen theory came in for a lot of criticism directed mainly at the implied predestination of tissues to specific histogens. Practically sharp distinction between dermatogen and periblem and between periblem and plerome was not seen. In some roots a fourth histogen, the **calyptrogen** has also been added and much later the term **columellogen** was also added to describe roots where the columella shows independent initials ontogenetically unrelated to the peripheral part of the root cap.

Schüepp (1917) proposed the Korper-Kappe concept in relation to the cell pattern at the apical meristems in roots. An initial cell first divides transversely followed by its daughter cells dividing longitudinally thus forming two cell files. This gives rise to a ‘T’ division or ‘T’ pattern and can occur in two ways. If the head of the ‘T’ faces the root apex or the centre of the root it is called the **Korper** pattern and if the head of the ‘T’ faces away from the centre of the root it is called the **Kappe** pattern.

![Fig. 27: Outline diagram showing Korper-Kappe divisions and different zones in the root apex based on cell net analysis](image)

Clowes (1954) put forward the **quiescent centre** concept. He described that at the distal tip of the root body, there is a central region of cells which divides rarely or not at all. This group of cells was termed quiescent centre. The peripheral cells surrounding this group are meristematic and are regarded as part of promeristem. Later many investigators supported the presence of a quiescent centre at the root pole but this was also suggested that it is not a permanent feature of all the roots. Experiments with radioactive tracers, irradiation of root tips differential staining, counting of mitotic figures, etc. have revealed that the cells of the quiescent centre have lower concentrations of RNA, DNA and protein, fewer mitochondria, little ER, smallest dictyosomes, nuclei and nucleolii than the surrounding cells. Clowes (1961) also put forward the concept of **promeristem** and described it as that part of the root apex which is capable of giving rise to all the tissues of the root.

**Four types** of root apices can be recognised based on the mode of origin of the cap and relation between initials/histogens and primary tissues of the root.

**Type I** - Both the root cap and root body are derived from a **single apical cell** and this type is commonly present in vascular cryptogams.
**Type II** – Here two groups of initials are present at the root pole, the inner group forming the plerome while the outer forming the periblem and cap. Thus the root cap and cortex have common origin. This type is generally seen in gymnosperms.

**Type III** – In this type there are present three groups of initials arranged in three tiers at the root pole. The innermost tier forms the plerome, the middle one forms the periblem and the outermost gives rise to the dermatogen and the cap. Here also the root cap and epidermis are common in origin. This type is generally seen in dicotyledons.

**Type IV** – Here, there are three or four groups of initials arranged in three or four tiers. The innermost tier gives rise to the central cylinder and the second tier below this forms the cortex (in case of four tiers of initials) or the cortex and the epidermis (in case of three tiers of initials). Thus the cap has its independent group of initials. This type is generally seen in monocots.

Guttenberg et al. (1955) based on arrangement of initials described **closed and open roots**. The roots with discrete initials are called closed and those with irregular group of cells as open. In closed roots atleast the central cylinder and columella arise from separate initials whereas in open roots these two regions arise from a common group of initials. Cortex may or may not have separate initials. Generally the epidermis and peripheral part of root cap arise from a **rootcap – epidermis complex** present on the periphery of the root pole. The closed roots may become open through a process of **opening out** and **knee formation** during ontogeny.
Differentiation of primary and secondary tissues

A vascular plant begins its life cycle in the form of a simple unicellular zygote. The zygote develops into the embryo and eventually into a mature sporophyte. This development occurs by division, enlargement and differentiation of cells and their organisation into more or less specialized complexes, the tissues and systems of tissues. After a certain period of vegetative growth, the plant enters into reproductive phase with the development of spore bearing structures.

The initial growth of the roots and vegetative and reproductive shoots is commonly termed as primary growth. This is brought about mainly by apical meristems. The plant body formed by this growth is the primary plant body consisting of primary tissues. In gymnosperms, most dicotyledons and some monocotyledons, an increase in thickness of stem and root occurs by means of secondary growth. The secondary growth is mainly brought about by vascular cambium which produces secondary vascular tissues resulting in an increase in diameter of the plant. In addition a cork cambium or phellogen develops in the peripheral region which
produces the **periderm**. The tissues produced by the vascular cambium and the phellogen are known as **secondary tissues** and they constitute **secondary plant body**.

The primary growth is completed in a relatively short period, whereas the secondary growth of an axis persists for a longer period.

**Primary Permanent tissues**

These are composed of cells which have lost the power of division completely or for the time being. These are formed by division and differentiation from the meristematic tissues particularly the apical meristems. The cells of these tissues may be living or dead and have thin walled or thick walled depending upon their types. The permanent tissues may be simple or complex.

**Simple tissues**

A simple tissue is made up of one type of cells forming a homogenous system of cells. The common simple tissue in plants are parenchyma, collenchyma and sclerenchyma.

1. **Parenchyma** - The parenchyma tissue is composed of living cells, generally having thin walls and polyhedral shape (Fig. 30A). These cells show variations in their morphology and physiology and are concerned with vegetative activities of the plant. Usually the cell wall is made up of cellulose. In storage region the walls of the cells may become thick due to deposition of hemicellulose. The parenchyma cells are isodiametric, thin walled and equally expanded cells. They are spherical, oval, rectangular or polygonal in shape possessing intercellular spaces in between them. They possess sufficient amount of cytoplasm and one or more nuclei. Most parts of various organs of plant body such as mesophyll of leaves, the pulp of fruits, endosperm of seeds, pith and cortex of stems and roots, and other organs of plants consist mainly of parenchyma. These cells occur in xylem and phloem also.

   In hydrophytes like *Hydrilla* etc., the parenchyma cells in the cortex possess well developed air spaces or air cavities which remain filled with air. Such a tissue is known as **aerenchyma** (Fig. 30C). The air cavities help the plant in floating. They also facilitate respiration. When the parenchyma is exposed to light, it develops chloroplasts and is known as **chlorenchyma** (Fig. 30B). It is found in leaves and other green organs of the plant and performs the function of photosynthesis. If the rod shaped chlorenchyma cells become parallely arranged and tightly packed, they are called **palisade**. If they become ellipsec and loosely arranged with large intercellular spaces, they are called **spongy tissue**. Palisade and spongy parenchyma are present in leaf mesophyll. In storage parenchyma walls become thick due to deposition of carbohydrates. Thick walled parenchyma is found in the endosperm of *Phoenix dactylifera*, *Asparagus* and *Coffea arabica*. 
Sometimes the parenchyma cells appear star shaped due to formation of long arms or branches (Fig. 30D). Such a parenchymatous tissue is called stellate parenchyma (e.g. petioles of leaves of banana). When the parenchyma cells become long and tapering at either end, they constitute prosenchyma. Specialized parenchyma cells which produce and store tannins, oils, crystals, etc. are termed as idioblasts.

**Functions** - Due to presence of active protoplast, the parenchyma functions as the seat of all essential vegetative functions like photosynthesis, storage of food materials, secretion, excretion, etc. Parenchyma cells associated with xylem and phloem help in the conduction of water and food materials. The turgid parenchyma cells help in giving rigidity to plant body. Epidermal cells with cutinised outer walls have protective function. Storage parenchyma store food in the form of starch grains, proteins, fats and oils. Chlorenchyma is responsible for photosynthesis and aerenchyma provide buoyancy to the plants. As the parenchyma retain the potentialities of cell division, it helps in vegetative propagation by forming adventitious roots and buds. It also helps in wound healing.

2. **Collenchyma** - Cells of this tissue are living with vacuolated protoplast. Chloroplast may also be present. The shape of cells is variable. Short collenchyma cells resemble parenchyma whereas longer ones may have tapering ends often overlapped and interlocked like fibres. These cells are usually polygonal in cross section. Their cell wall
is unevenly thickened. The thickenings are localized specially at angles. Some simple pits are also found on the walls. The thickening is due to deposition of cellulose and pectic materials with high percentage of water. The cells are extensible and are strong enough to provide tensile strength to the organs. It is the primary mechanical tissue of dicotyledons and usually absent in monocotyledons. Collenchyma occurs in the peripheral portions of rapidly elongating organs like young stems, floral stalks, petioles of leaves, etc. They occur in form of homogenous bands beneath the epidermis, or they may occur as discontinuous patches. In leaves they may be differentiated on one or both sides of the veins and along the margins of the leaf blade. On the basis of pattern of thickening of cell wall and arrangement of cells, three types of collenchyma have been recognised. These are:

Angular - In these cells thickenings are present at corners and cells are irregularly arranged. E.g. collenchyma tissue found in stems of Datura and tomato (Fig. 31B).

Lacunar or tubular - These cells possess small intercellular spaces, e.g. hypodermis of Cucurbita stem (Fig. 31C).

Lamellar - These cells possess thickenings at their tangential walls. Here the cells lie in tangential rows, e.g. hypodermis of sunflower stem (Fig. 31D).
Functions - The chief primary function of collenchyma is to give support to the plant body. In growing organs it provides tensile strength till more effective mechanical tissues (e.g. sclerenchyma) are differentiated. This tissue is present in the peripheral parts of plant so it resists the bending and pulling action of wind. In some plants collenchyma regain the power of division, e.g. in those plants where cork cambium develops in the collenchymatous hypodermis. In such cases it forms secondary tissues.

3. Sclerenchyma - The sclerenchyma tissue consists of thick walled cells, often lignified, whose main function is to provide mechanical support to the plant body. At maturity these cells become strong and hard. Their cytoplasm disappears and they become dead. Usually they are found in old parts of the plant. On the basis of length of cells and quantity of deposition of wall material, they are of two types.

   (i) Fibres - These are elongate sclerenchyma cells usually with pointed ends. They usually possess lignified walls with small, round or slit-like and often oblique pits (Fig. 32A, B). In mature cells the protoplast disappears and they become dead and empty. They may occur in patches, in continuous bands or singly in pericycle, xylem, phloem etc. They provide strength and rigidity to the various organs of the plants. The average length of fibres is 1-3 mm in angiosperms. In some plants like
hemp, flax, jute, ramie, etc. the fibres are of excessive lengths ranging from 20 mm to 550 mm. These long and thick walled cells are used as fibres for commercial use.

The fibres that constitute an integral part of xylem are called xylary fibres or wood fibres. The extraxylary fibres include phloem fibres originating in primary or secondary phloem, cortical fibres originating in the cortex and perivascular fibres present in the peripheral region of the vascular cylinder inside the innermost cortical layer but not originating in the phloem. The extraxylary fibres are sometimes combined into a group termed bast fibres.

(ii) Sclereids - These cells are usually isodiametric but some may become elongated also. Sometimes they are spherical, cylindrical, dumbell-shaped or even stellate. Their cell wall becomes highly thickened sometimes obliterating the cell cavity. The mature sclereid cells are devoid of living contents. Apart from their shape and size they differ also from sclerenchyma fibres in that they originate from parenchyma cells by continued thickening and lignification of the cell wall whereas the fibres from meristematic cells. Usually they are found in the cortex and pith but are also common in leaves, fruits and seeds of gymnosperms and dicotyledons.

Foster (1949) categorised the sclereids into following four types -
(i) **Brachysclereids or stone cells** - These are shorter and roughly isodiametric cells (Fig. 33A). They are usually found in the cortex, pith and phloem of stems (e.g. *Cinnamomum*) and fruit pulp (e.g. *Pyrus*).

(ii) **Macrosclereids or rod cells** - These are elongated columnar sclereids and are chiefly found in the outer seed coat layers of many members of the family *leguminoseae* (Fig. 33B).

(iii) **Osteosclereids or prop cells** - They are bone or barrel shaped with dilated ends, e.g. leaf of *Hakea* and *Osmanthus fragrans* (Fig. 33C).

(iv) **Astrosclereids** - These are star shaped or stellate cells found in leaves of *Nymphaea* and the stems and leaves of *Thea* and *Trochodendron* (Fig. 33D).

(v) **Trichosclereids** - These are hair – like, sometimes branched sclereids and are found in the intercellular spaces in the leaves and stems of certain hydrophytes, in the aerial roots of *Monstera* and in the leaves of olive (Fig. 33E).

**Complex tissues**

These tissues are made up of more than one type of cells working together as a unit to perform a particular function. Xylem and phloem which together form the **vascular tissue**, are the two principal types of complex tissues.
Xylem

It is also known as hadrome. It is a conducting tissue which conducts water and mineral salts to different parts of the plant. It is composed of several types of living and nonliving cells. The elements or principal cell types of xylem are tracheary elements (tracheids and vessels), xylem or wood parenchyma and xylem or wood fibres.

1. **Tracheary elements** - Conduction in the xylem is performed by two types of tracheary elements - tracheids and vessels. The main difference between the two is that the tracheid is non-perforated while the end walls of the vessels are perforated. A vessel or trachea is built of numerous vessel members joined together and transverse walls dissolved.

Tracheids are present in all vascular plants, whereas vessels are confined to angiosperms with the exception of some primitive groups. Xylem is called the primary xylem if its elements are derived from the procambium of the apical meristem. When it is derived from the vascular cambium during secondary growth, it is called secondary xylem. The earlier formed xylem is called protoxylem and the later formed is called metaxylem.

Tracheids - The tracheid is a fundamental element in xylem. These are more or less elongated cells having tapering, rounded or oval ends. They are nonliving cells devoid of living protoplast at maturity. Their walls are hard, moderately thick and usually lignified. In a cross section the tracheids appear angular though rounded forms also occur. They have a wide cell cavity or the lumen without any contents. They have secondary wall thickenings (Fig. 34) in different manners and on the basis tracheids may be called annular (thickening in form of rings), spiral (in form of helices) scalariform (in form of a ladder) reticulate (in form of a network) or pitted (entire surface is thickened except for uniformly distributed pits). Number and arrangement of pits may vary on different walls of the same cell.

Tracheids remain arranged parallel to the longitudinal axis of the plant. Besides conduction of water they provide mechanical strength to the plant.
Tracheary elements possess two types of pits, **simple** and **bordered**. There are the areas through which diffusion of fluid takes place from cell to cell. The simple pits are the areas having only primary wall. There is no secondary thickening. So at the region of the pit the only wall between the two cells is the primary cell wall together with the middle lamella. It is termed as the **pit membrane**. The bordered pits, are however more complicated as the secondary wall arches from both sides. As a result a dome shaped body is formed which is represented by two circles, the smaller one forming the pit aperture and larger one inside forming the pit cavity or pit chamber. In front view, the pit cavity forms a border round the pit aperture and hence the name. The pit membrane is as usual consists of primary walls of two cells and the middle lamella. The central part of the pit membrane swells up to form a **torus**. Due to changes of pressure the torus can shift its position and come to the mouth of the pit, and thus block the pit aperture. The torus is very well developed in the bordered pits of gymnosperms, and is surrounded by bundles of microfibrils known as **margo**.

**Fig. 34**: Diagram depicting various types of thickenings on the walls of tracheids and vessels (A) Annular (B) Spiral (C) Scalariform (D) Reticulate (E) Simple pitted (F) Bordered pitted
Vessels or tracheae - These are long cylindrical and tube-like structures with lignified walls. They are composed of a row of cells, placed one above the other. The vessels are formed by partial or complete dissolution of the transverse walls or end walls of cells. Dissolution of the transverse walls takes place during the development of the vessels. They are wider than tracheids. The openings in vessel element walls are known as perforations. These openings are restricted to the end walls except in certain slender tapering types. The area formed is known as perforation plate. The perforation plate is called simple if the entire end wall dissolves and there is a present single pore. In some plants (Liriodendron) the end walls between the cells do not dissolve completely and the perforation plate is multiple because it has many pores. If the pores remain in a ladder-like manner the multiple perforation is termed as scalariform. If it is in the form of a network it is known as reticulate perforation. If a group of circular holes is formed it is termed as foraminate. Simple perforation plate is treated to be an advanced type.
Like tracheids, walls of vessels also possess annular, spiral, scalariform, reticulate or pitted thickenings. The protoxylem vessels generally have annular and spiral thickenings. In the young and developing vessels the cytoplasm is dense. After the laying down of secondary wall material the cell organelles break down and mature vessels become dead, are without cytoplasm and possess a wide central lumen.

These cells remain arranged parallel to the longitudinal axis of the plant. Their function is to conduct water and to provide mechanical support. As compared to tracheids, they are more efficient to conduct water and minerals due to presence of perforation plates.

The vessels are present in almost all the angiosperms. They are not found in gymnosperms (exceptions are Gnetum, Welwitschia and Ephedra) and Pteridophytes (exceptions are Pteridium and some species of Selaginella and Equisetum).

**Ontogeny of a vessel** - A vessel or trachea originates from a row of meristematic cells of procambium or vascular cambium. These cells remain arranged in a longitudinal series. As usual the cells grow and secondary walls are laid down, some areas of primary walls remain uncovered which later disintegrate to form perforations. The protoplast in the mean time becomes more and more vacuolated and ultimately dies and disappears. Due to deposition of pectic substances, the primary wall swells up and ultimately breaks down, thus forming the continuous tube like vessel. Unlike a tracheid, a vessel arises from a group of cells.
2. **Xylem fibres or wood fibres** - These are sclerenchyma cells which remain associated with other xylem elements and they are mainly meant mechanical support. Fibres are very much elongated and are usually dead cells with extremely thick lignified walls and narrow lumen. The wood fibres can be derived from tracheids. The fibres that are in a transition stage are termed as **fibre tracheids**. The fully developed wood fibres are termed as **libriform fibres**. These are narrow ones with highly thickened secondary walls and simple pits. Their central lumen is almost obliterated.

![Fig. 37: Developmental stages of perforations in a vessel](image)

![Fig. 38: A&B - L.S and T.S. of fibre tracheid; C&D - L.S. and T.S. of libriform fibre; E&F - L.S. and T.S. of septate fibre tracheid](image)
3. **Xylem parenchyma or wood parenchyma** – These are living parenchymatous cells which remain associated with other xylem elements and derive their origin from the same meristem. These cells have thin walls enclosing living contents. Their walls are made up of cellulose and possess pits. They are found associated with primary as well as secondary xylem.

![Fig. 39: Wood parenchyma](image)

A&B - L.S. and T.S. of wood parenchyma from *Quercus alba*; C&D - L.S. of T.S. of wood parenchyma from *Carya ovata*

The main function of these cells is to store starch and fatty food, other matters like tannins, crystals etc. may also be present. As a constituent of xylem, they also help in conduction of water.

**Phloem**

It is another specialized complex tissue and is also known as **leptome** or **bast**. The main function of phloem is to translocate food materials from green parts, where they are synthesized to other parts of the plant. Phloem is composed of four kinds of cells: 1. Sieve elements 2. Campanion cells 3. Phloem fibres 4. Phloem parenchyma

**Sieve elements** - The most important constituents of phloem are the **sieve tubes** and **sieve cells**. Ontogenetically, a sieve tube resembles a vessel and a sieve cell a tracheid.

1. **Sieve tubes** - These are long and tubular structures with wide cell lumens. Their cell walls are made of cellulose. Sieve tubes are formed by end to end joining of many cells arranged in longitudinal series. The end walls or transverse walls of these cells are
perforated in a sieve-like manner. The perforated end walls are called the **sieve plates** which contain perforations or sieve areas through which cytoplasmic connections are established between adjacent cells. Usually the sieve plates are obliquely placed. Their cytoplasm occurs in form of a thin lining layer along the inner side of the cell walls enclosing a big central vacuole. Plastids are also present in the protoplast.

The most important characteristic feature of the sieve element protoplast is its development. During differentiation, the nucleus disorganises. It is the only living functioning element which lacks nucleus.

![Diagram of sieve tubes and companion cells](image)

**Fib. 40 : Sieve tubes and companion cells**  
A - Longitudinal section, B - Transverse section

Sieve plates may be simple when they consist of one region of pores (*Cucurbita*) or compound when there are several such regions separated by bars or wall thickenings (*Vitis*). In most cases, the perforations in the sieve plates are surrounded by a carbohydrate of unknown chemical composition called the **callose**. During autumn, the callose is deposited as the sieve pores and the sieve tubes become nonfunctional. On the onset of spring or active season the callose is dissolved and the pores are reopened. As a result the sieve tubes become functional again. The sieve tubes may become permanently nonfunctional if the callose is deposited permanently. Sieve tubes are absent in pteridophytes and gymnosperms.

**Sieve Cells** - These are comparable to the tracheids. They are narrow elongated cells without conspicuous sieve areas. They usually have oblique walls. Sieve cells are more primitive than sieve tubes. They occur in lower vascular plants and gymnosperms.
2. **Companion cells** - They are specialized parenchyma cells which remain associated with the sieve tubes of angiosperms. Their longitudinal walls are provided with pits. They are closely associated in origin, position and function with the sieve tube elements. Both the sieve tube element and its associate, the companion cell originate from the same meristematic cell. Their functional association is proved by the fact that companion cells survive with the disorganisation of sieve tubes. Companion cells have dense cytoplasm, large nuclei and thin cellulosic cell wall. In transsection they appear as small, triangular, rectangular or polyhedral in shape. The companion cells and sieve tubes have close cytoplasmic connections through numerous pits and plasmodesmata present in the common walls. These cells maintain the pressure gradient in the sieve tubes. They are supposed to assist the sieve tubes in translocation of food. Companion cells occur abundantly in angiosperms particularly in the monocotyledons. They are absent in some primitive dicotyledons, pteridophytes and gymnosperms. In pteridophytes and gymnosperms some small parenchymatous cells called as alburnous cells are present which are comparable to companion cells of angiosperms.

3. **Phloem fibres** - These are sclerenchymatous fibres constituting a part of phloem. These are dead, elongated cells having interlocked ends and lignified walls with simple pits. They provide mechanical strength to the plant. These fibres are very strong and are used for manufacturing of ropes and cords.

4. **Phloem parenchyma** - These are living cells and remain associated with sieve elements. Their structure is similar to normal parenchymatous cells. Usually they perform the function of storage of organic food matters. Tannins, crystals, etc. may also been present in them. They are absent in monocotyledons.

**Secondary tissues**

In most dicotyledons and gymnosperms, the primary permanent tissues make the fundamental parts of the plant and the further growth in thickness is completed by the cambial activity, i.e. the secondary growth in thickness. The tissue formed during secondary growth are called secondary tissues. This growth is due to the activity of two lateral meristems the **vascular cambium** and the **phellogen or cork cambium**. Secondary tissues may be of two types - the **vascular tissues**, formed by vascular cambium in the stelar region and **cork and phelloderm**, formed by phellogen in the extastelar region.

**Secondary xylem**

The vascular cambium forming the secondary xylem and secondary phloem, is composed of two types of cells - **fusiform initials and rays initials**. Fusiform initials are long, vertically oriented cells with tapering ends. These cells produce secondary xylem and secondary phloem. The ray initials are small isodiametric cells which produce secondary medullary rays. Activity of these initials results in the formation of two types of systems in the secondary xylem, the **axial** (vertical) and the **ray** (horizontal) systems. The horizontal system comprises the xylem rays and the vertical or axial system, the tracheary elements, fibres and wood parenchyma.

Unlike the procambium and the primary xylem have a haphazard cell arrangement and the cambium and the secondary xylem have an orderly arrangement of cells. In secondary xylem the cells are aligned parallel with the radii of the secondary body.
The secondary xylem consists of abundant vessels (having scalariform and pitted thickenings), tracheids, wood fibres and wood parenchyma. Usually the vessels have pitted type of wall thickening shorter than those of primary xylem. Annular and spiral tracheids and vessels are altogether absent. Xylem parenchyma cells are generally longer than the ordinary parenchyma. They may occur independently or in association of the vessels. The sclerenchyma fibres found in xylem show thick walls and bordered pits.

![Image of secondary xylem and phloem showing continuous rays through the cambium]

**Xylem rays**

The xylem rays are strap-like structure extending radically in the xylem. They are formed by ray initials of the cambium. These rays pass through the cambium and phloem as a continuous band forming a continuous conducting system. As a result of continuous divisions in cambial cells, these rays increase in length indefinitely. They resemble with pith rays of herbaceous dicotyledonous stems and hence are called medullary rays or pith rays. But they may be best called vascular rays, as they are compound structure of vascular tissues, xylem and phloem. These rays establish communication with the living cells of the vascular tissues and help in conduction of water and food from phloem to the cambium and xylem parenchyma. They also help in exchange of gases.

**Annual rings or growth rings**

Activity of cambium is directly influenced by environmental factors. Places where pronounced seasonal variations are found, the cambial activity is not uniform throughout the year. The wood formed during autumn and spring are quite different from each other. Activity of all plants increases during spring (the favourable reason for growth) and the cambial cells divide at a faster rate forming comparatively thin walled broader xylem elements. Tissues formed during the spring collectively form the spring wood or early wood. On the other hand, during winter and autumn (i.e. unfavourable seasons for growth), the cambium is lesser active forming lesser amount of xylem as compared to spring season. These vessels are thick walled with narrow lumen and the wood contains more tracheids and wood fibres. This wood is called autumn wood or late wood and is dark in colour. Spring and autumn woods remain arranged in the form of concentric rings. One ring of each spring and autumn wood combine to constitute an annual ring.
or growth ring. Each annual ring represents growth of one year. Age of a particular plant can be calculated by counting the annual rings. Counting is done from the basal part because the number of annual rings is lesser in the upper part of the plant. The determination of age of a tree by counting the annual rings is called dendrochronology. Trees growing in regions where there are no climatic changes throughout the year, do not exhibit annual rings. Sometimes adverse climatic or other unfavourable conditions (drought, defoliations, disease etc.) prevail during the middle of a growing season resulting in formation of more than one annual rings. These are called false annual rings.

![Diagram of tree cross-section](image)

**Fig. 42: A part of old dicotyledonous stem**

**Heart Wood and Sap Wood**

Secondary growth results in the formation of a considerable amount of secondary xylem in plant. In old trees, cells of central region of xylem become filled with oils, resins, tannins, gums etc. These cells die and become hard making the central region hard, durable and dark brown or blackish in colour. This is called **heart wood** or **duramen**. The function of heart wood is no longer of conduction, it gives only mechanical support to the stem. In many plants, inside the vessels of this region, balloon like structures are formed by xylem parenchyma cells. These structures are called **tyloses**. As the tylosis grows further, it is detached from the parenchyma cell from which it has been derived. In conifers, cavity of resin canal is closed by enlargement of epithelial cells. These enlarged cells are called **tylosoids**. Outside the heart wood the peripheral portion consists of lightly coloured tissues which include living cells also in the association of vessels and fibres. This part is called **sap wood** or **albernum** and it performs the physiological activities, such as conduction of water and nutrients and storage of food, etc. As the plant grows older, rings of sap wood bordering heart wood gradually keep converting into heart wood.
Porous and nonporous wood

Wood of dicotyledonous plants which has vessels in the xylem is known as porous wood or hard wood. The gymnospermous wood which lacks vessels is called as nonporous or soft wood. When vessels occur in the wood and exhibit a ring-like arrangement in transection, the wood is called ring porous. If the vessels are uniformly distributed throughout the wood, the wood is called diffuse porous.

Periderm

Secondary tissues formed by activity of vascular cambium exert pressure on primary tissues. As a result primary xylem, pith etc. are pressed towards the inner side and ultimately cells of these tissues are crushed. Tissues present outside the secondary phloem are pushed towards periphery. The epidermis gets stretched and before it ruptures, the protective function performed by primary tissues is taken over by a new secondary tissue called periderm. The periderm consists of the phellogen or cork cambium, the phellem or cork cells and the phelloderm or secondary cortex. Usually the cork cambium is differentiated in the hypodermis but sometimes it differentiates in the epidermis (apple), pericycle (Clematis) or phloem (Vitis).

The cork cambium is a secondary meristem. Its rectangular cells divide and form cells on either sides i.e. centripetally and centrifugally. Cells towards periphery collectively form the cork or phellem. Mostly the cells formed towards inner side are parenchymatous. Sometimes they are collenchymatous or sclerenchymatous. These cells constitute the phelloderm.

Normally the phellogen produces more amount of phellem on the outer side than phelloderm on the inner. The phellem or cork cells remain arranged in distinct radial rows. They are compactly arranged. After differentiation, they loose protoplasts and become dead. The cells remain filled with air and coloured organic matters. They are strong and provide protection to the inner tissues and mechanical strength to the plant.

A thick layer of suberin is deposited next to the primary walls making these cells impervious to water and gases. The cells of phelloderm resemble those of cortex as these are living,
isodiametric and have intercellular spaces. But they remain arranged in definite radial rows. These cells perform the function of photosynthesis and storage of food.

![Diagram of Periderm Formation]

**Fig. 44: Periderm formation**

**Bark**

This tissue may be present in very old roots of trees. Generally, the term bark is applied to all tissues external to the vascular cambium.

The periderm is formed by one or many layers of phellogen. The first phellogen differentiates in different cell layers external to the vascular cambium. It may develop in living parenchyma or collenchyma cells of the epidermis or hypodermis. Sometimes new phellogen layers may arise in the deeper regions of cortex, pericycle and even phloem. The phellogen, after its formation, continuously produces cork on outer side and phelloderm on inner side. The first phellogen may remain active for sometime to several years. In many plants successive phellogen may also develop producing successive periderms. Since the cork cells are suberized, they prevent the outward supply of water and food. Eventually all the living cells (including previously formed periderms) present on the outside of the inner phellogen become dead. These dead tissues forming a crust may separate from the axis in the course of time or may remain as hard crust on the stem for several years. The dead tissues outside the innermost phellogen are called as rhytidome or outer bark which includes all cork layers and dead cortical layers and phloem tissue and the living part of the bark inside the rhytidome is called the inner bark. In certain plants the additional periderms are formed in the form of scale like layers so that the outer dead tissues are separated in the form of small pieces, which are called scale bark. When successive rings of phellogen are formed generating concentric rings of dead tissues, it is called ring bark.

**Lenticels**

Due to formation of periderm with dead cork cells with suberised walls, the gaseous exchange between the internal living cells and outer atmosphere becomes difficult. To replace this, some pores in the form of raised spots develop on the surface in between the dead cells of phellem. These pores are called lenticels. Usually they are formed beneath the stomata. The phellogen present at these places form parenchyma cells instead of cork cells towards the substomatal chamber. These rounded thin walled cells form a group of loosely arranged cells known as complementary cells. Increase in the number of complementary cells results in rupturing of epidermis. The newly formed tissue protrudes above and looks like lens shaped raised spot. Often the phellogen forms masses of compactly arranged cells known as closing cells alternating with loosely arranged complementary cells. Activities like transpiration and exchange of gases between atmosphere and internal tissues of plant are carried out by the lenticels.
Secondary phloem

Usually the phloem elements are produced in lesser number than that of xylem elements. The elements of secondary phloem show arrangement similar to xylem elements. They remain arranged in two systems, vertical and horizontal. The sieve tubes, companion cells, phloem parenchyma and fibres which originate from the fusiform initials of the cambium form vertical system and are responsible for vertical conduction of food matters. The ray parenchyma cells formed by the ray initials constitute the horizontal system.

The secondary phloem is a more complex tissue having a longer functioning life as compared to the primary phloem. The cells of secondary phloem remain arranged in radial rows. It’s sieve tubes are produced in larger number, they are shorter and the fibres are more abundant. The sieve tubes do not show any regularity of distribution and they usually possess simple sieve plates. One or more companion cells may extend along the entire length of the sieve tube. In younger stages abundant parenchyma is present which decreases in number at maturity. The parenchyma cells help in vertical conduction of food matters and also serve in storage of starch, crystals and other materials. Sclerenchyma is characteristic of secondary phloem, occur abundantly in form of discrete bands, isolated patches or even singly. Sclereids are also found either independently or in association with the fibres. During the course of time some phloem elements become nonfunctional. In nonfunctioning phloem some parenchyma cells elongate, undergo sclerosis and form fibre-like elements known as fibre sclereids. The phloem rays are formed by ray initials of the cambium and they form the horizontal system of the tissue. At the time of formation, xylem and phloem rays are equal in width. The width of phloem rays increases with the maturity of the plant. They may be uni- or multi-seriate. The phloem rays are smaller than the xylem rays. Unlike xylem the phloem formed during early and late growing season do not show any distinction.