Botany and Microbiology Department

Lectures in

Botany 3

“ Plant anatomy and physiology”

Prepared by
Prof.Dr./ Noha Ahmed El-Tayeh
Dr/ Nora Hassan Yossif

2nd year Biology and geology students
First term
2022/2023

Basic data

College: **Science**

year: **second**

Specialization: **Biological and Geological Sciences**

Number of pages: **236**

The department to which the course belongs:

Department of Botany and Microbiology

Contents

Advanced plant anatomy

- Tissue structure (meristematic and permanent tissues)
- Simple and compound tissues
- Steller structure and development
- Evolution of vascular system
- Primary plant body and types of stems
- Secondary plant body
- Various types of secondary thickening (normal and abnormal)

Part I

Advanced plant anatomy

Introduction

MERISTEMS " IN THE early stages of the development of the embryo, all the cells undergo division, but with further growth and development cell division and multiplications become restricted to special parts of the plant in which the tissues remain embryonic in character and the cells retain the ability to divide. These embryonic tissues in the mature plant body, are called meristems. Cell division can also occur in tissues other than meristems, for instance, in the cortex of the stem and in young, developing vascular tissues. However, in these tissues the number of divisions is limited. On the other hand, the cells of the meristems continue to divide indefinitely and as a result new cells are continually added to the plant ·body. Meristems may also be found in a temporary resting phase, for instance, in perennial. plants that are dormant in certain seasons and in axillary buds that may be dormant even during the active phase of the plant. The process of the growth and morpho-physiological specialization of the cells produced by the meristems is called differentiation. Theoretically, it was believed that the tissues that undergo differentiation gradually lose the embryonic characteristics of the meristem and acquire the mature state. Such tissues are called mature or permanent. Recently it has been shown that the term permanent tissues. Can only be used in relation to certain cells which have undergo irreversible differentiation, for instance, sieve elements which have no nucleus and dead cells, such as tracheids, vessel elements and cork cells. All cells which contain nuclei possess, to 'a certain degree, the ability to grow and divide and dedifferentiate if the appropriate stimulus is present (Bloch, 1941; Buvat, 1944, 1945; Gautheret, ,1945,1957; White, 1946; Wetmore, 1954, 1956).

Classification of meristems The classification of meristems is made on the basis of various criteria -their position in the plant body, their origin and the tissues which they produce, their structure, their stage of development and their function. According to the position of the meristems in the plant body they are divided into the following types: (a) apical meristems, which are found in the apices of the main and secondary shoots and roots; (b) intercalary meristems, which are found between mature tissues~ as, for example, in the bases of the internodes of grasses; (c) lateral meristems, which are situated parallel to the circumference of the organ in which they are found, as, for instance, the vascular cambium and the phellogen. It is customary to distinguish between primary and secondary meristems -a classification based on the origin of the meristems. Accordingly, primary meristems are those whose cells develop directly from the embryonic cells and so constitute a direct continuation of the embryo, while secondary meristems are those that develop from mature tissues which have already undergone differentiation. The above definitions of primary and secondary meristems, however, are not always accurate. For example, the apical meristems of truly adventitious organs develop secondarily within relatively mature tissues as well as within secondary meristematic tissues, although according to their structure and function they are primary meristems. On the other hand, a large part of, or sometimes even the entire, vascular cambium, which is generally accepted to be a secondary meristem, develops. at a late stage, from the "apical meristem, i.e. from a part of the procambium. Examples of secondary meristems, which can be determined as such ·without doubt, according to origin, are the phellogen which develops from parenchyma or collenchyma cells which have already undergone differentiation and callous tissue which develops in tissue cultures made from mature tissues. From the above it can be seen that it is more correct to use the terms primary and secondary meristems to refer. to. the stage of development at which the meristems appear and to the types of tissue that develop from them and not to their origin. From the primary meristems the fundamental part of the plant, such as the epidermis, the cortical tissues of the stem and root, the mesophyll of the leaf and the primary vascular tissues develop, and from the secondary meristems the secondary vascular and protective tissues. In certain monocotyledons, such as some palms, banana and others, the thickening of the stem takes place near the apices and therefore is regarded as being of primary nature. The meristem responsible for this type of increase in thickness is termed primary thickening meristem.

MERISTEMATIC TISSUES

Growth of an organism consists of increase in the protoplasmic body. This increase is associated with differentiation of new cells. In higher plants growth is caused by new cell formation followed by cell enlargement and differentiation of the new cells. Formation of new cells is chiefly localized in certain regions known as meristems.

The term meristem is used to describe regions of continuous cell formation.

The term meristematic is used for cells and tissues that have characteristic of meristem, especially cell division, but do not themselves constitute meristem.

The term embryonic describes the meristematic tissue of the embryo.

The meristematic cell is characterized by the following:

1- Abundant cytoplasm.

2- Large nucleus.

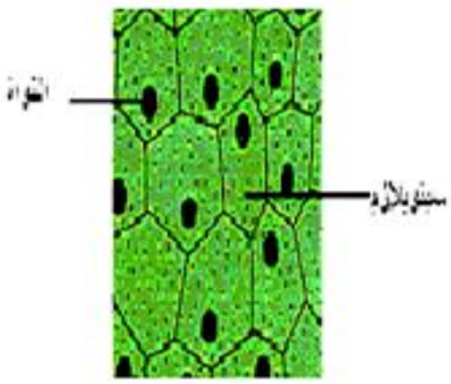
3- Thin primary wall of cellulose.

4- No intercellular spaces.

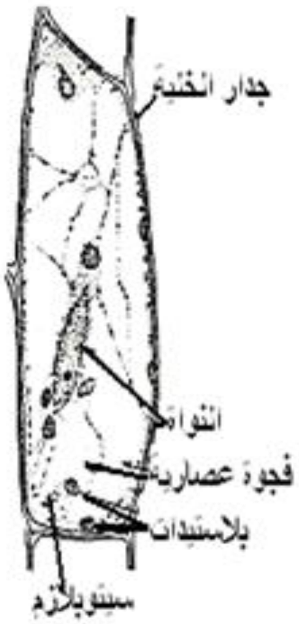
5- No drastic substances.

6- Small or lacking vacuoles.

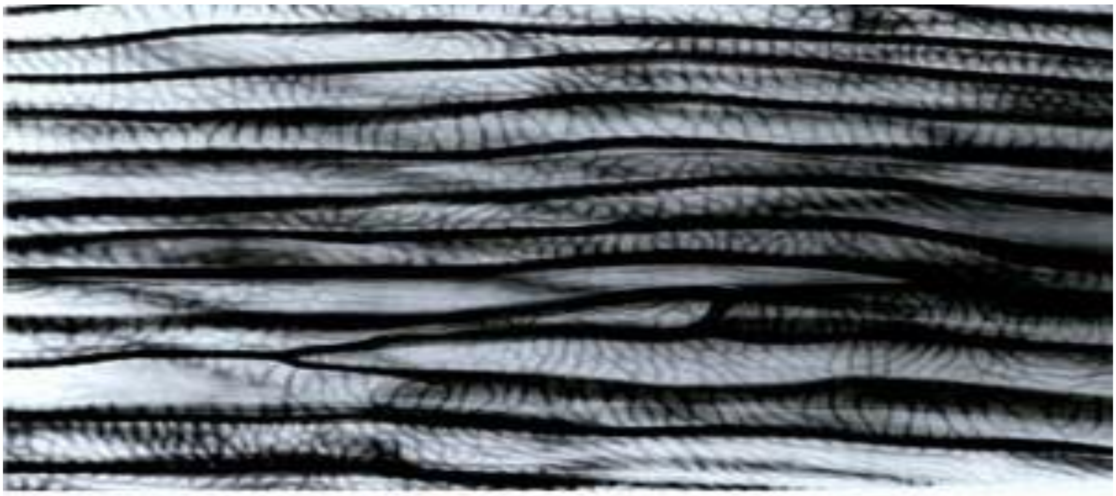
7- Activity dividing.



خلايا مرستيمية



خلية بالغة



Campsis radicans seed wing clearing. Lersten, Krueger and Curtis. 2002 Int. J. Plant Sci. 163: 369-378.

Meristematic tissues

Classification of meristems:

Meristems are classified in several basis:

1- Stage and method of development.

2- Method of division.

3- Origin of initiating cells.

4- Position in plant body.

5- Function.

1- Meristems based on stage and method of development:

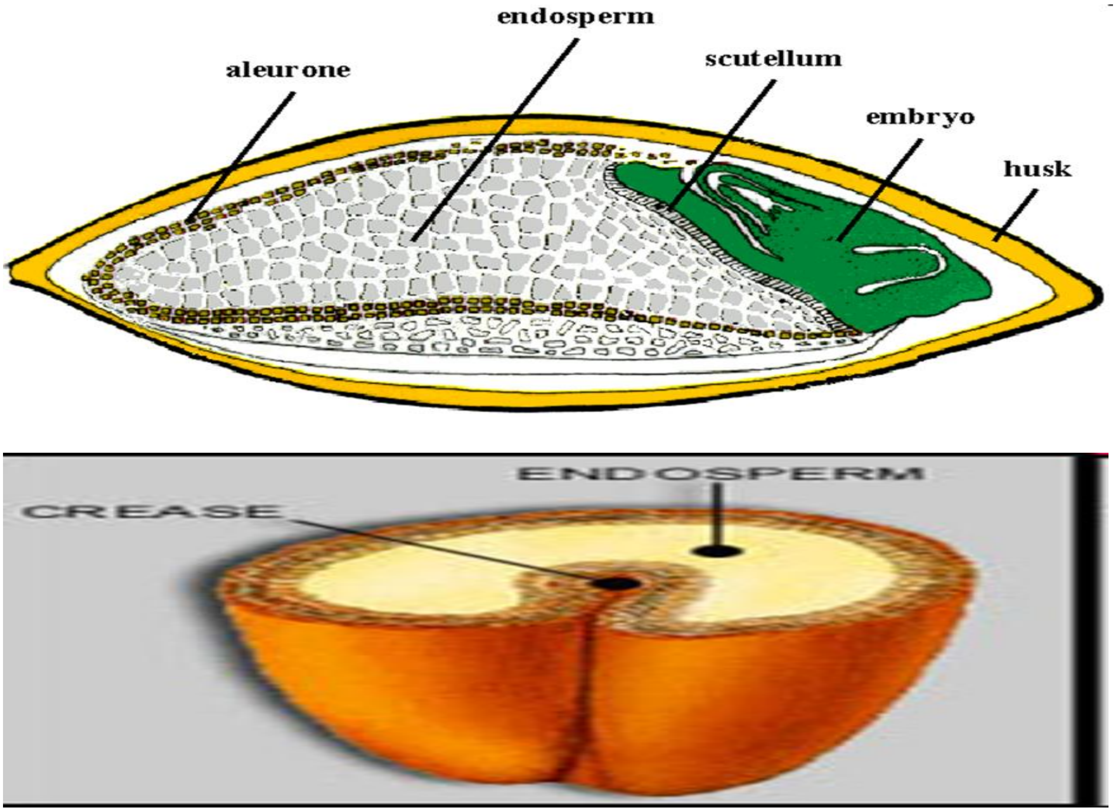
Promeristem: The region consists of young cells (meristematic cells) of similar shapes, sizes and diameters and is present at the extreme tip of roots and stems. As soon as cells of the promeristem begin to change in size, shape, wall and cytoplasm characteristics and start to differentiate they are not typical promeristem. **Examples of promeristems is root and stem tips and embryos.**

2- Meristems based on method of division:

a- Mass meristem: In which division occurs in three planes and produces increase in mass, for example, the meristems of embryos and seed endosperm.

*Anticlinal plane of division is situated approximately at right angles to the outer surface of plant part.

- Periclinal plane of division is running parallel to the surface of plant part.



MASS Meristem

Plate Meristem

Rib Meristem

b- Plate meristem: Division occurs in two plans so that plate like increase in area occurs, for **example**, meristem forming epidermis, and development of leaf-blade.

c- Rib meristem: Division occurs anticlinally in one plan producing columns of cells, therefore increase in length occurs for **example** leaf petioles and elongate of the stem.

3- Meristems based on their origin:

Primary meristems: These are meristematic regions derived from promeristem. They are present at the root and stem apices. Primary meristem is usually differentiated into zones in which the meristematic cells vary in size. Its cells differentiated and build up the primary permanent tissues, which make up the fundamental structure of the plant body.

Secondary meristem: They originate from permanent tissues which are transformed into meristematic cells. When cells of secondary meristem differentiate, they give rise to 2ry permanent tissues. Example of secondary meristem is **the cork cambium** which is formed from permanent tissues (epidermal, cortical or phloem cells) that reverted to the meristematic condition. Primary meristems build up the primary plant body, but the 2ry meristems add to the primary body 2ry tissues.

The vesicular cambium of the stem does not fall in any of the two groups. **It arises from promeristem** but **differentiates to give 2ry vascular tissue**. The cambium of roots and the interfascicular cambium of the stem are 2ry meristems.

4- Meristems based on position:

a- Apical meristems: Occur at the tips of the roots and stems of vascular plants. The activity of these meristems causes increase in length of the organ and forms the 1ry plant body.

b- Intercalary meristems: Portions of the apical meristems that have been separated from it by layers of permanent tissues. They are present in the stems of grasses and other monocots at the base of internodes. Their activity results in increase in length. This meristem is generally soon or ultimately become transformed into permanent tissues.

c- Lateral meristem: They are meristematic regions arranged parallel to the sides of the organ such as stems and their activity results in increase in diameter due to the periclinal division. Examples of this type are the vascular cambium which gives 2ry vascular tissues and the cork cambium which gives rise to cork.

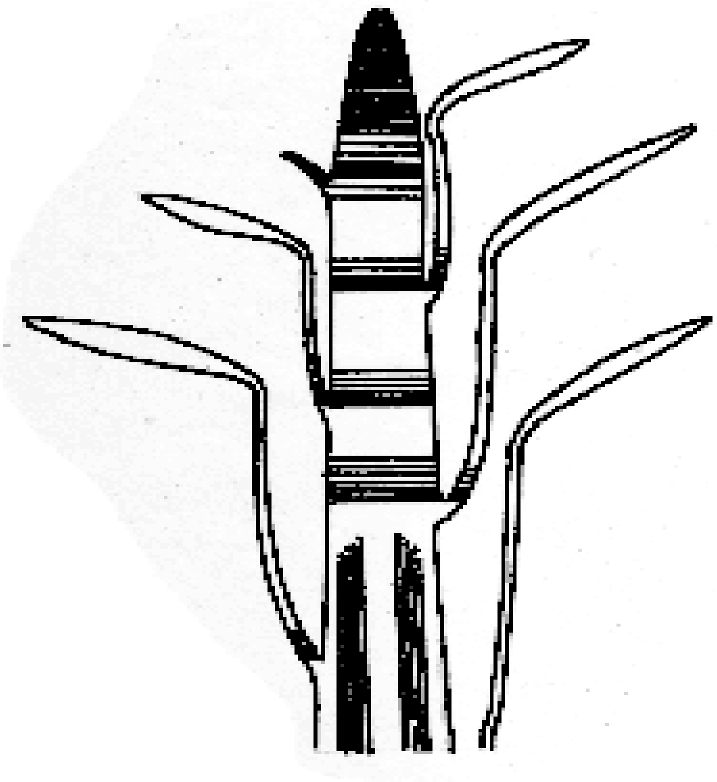
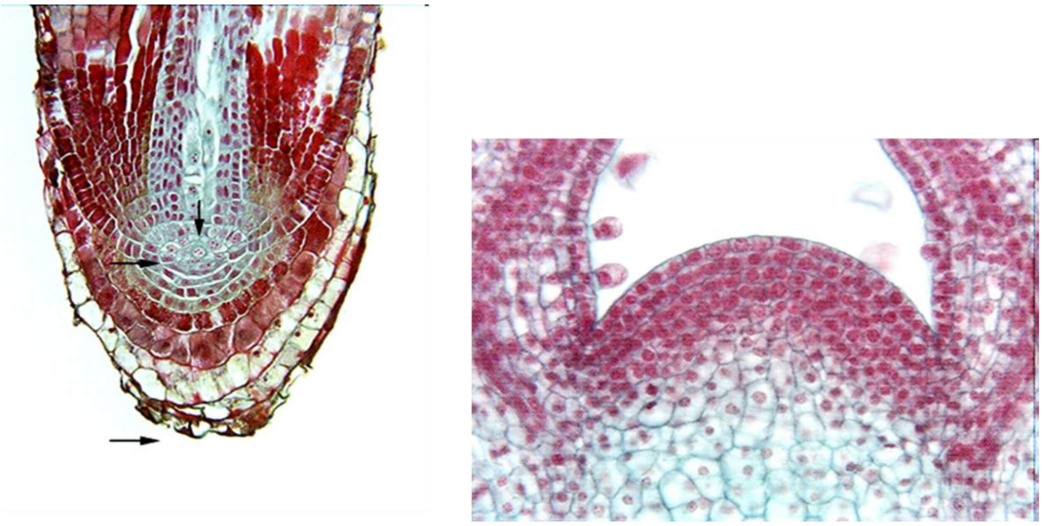
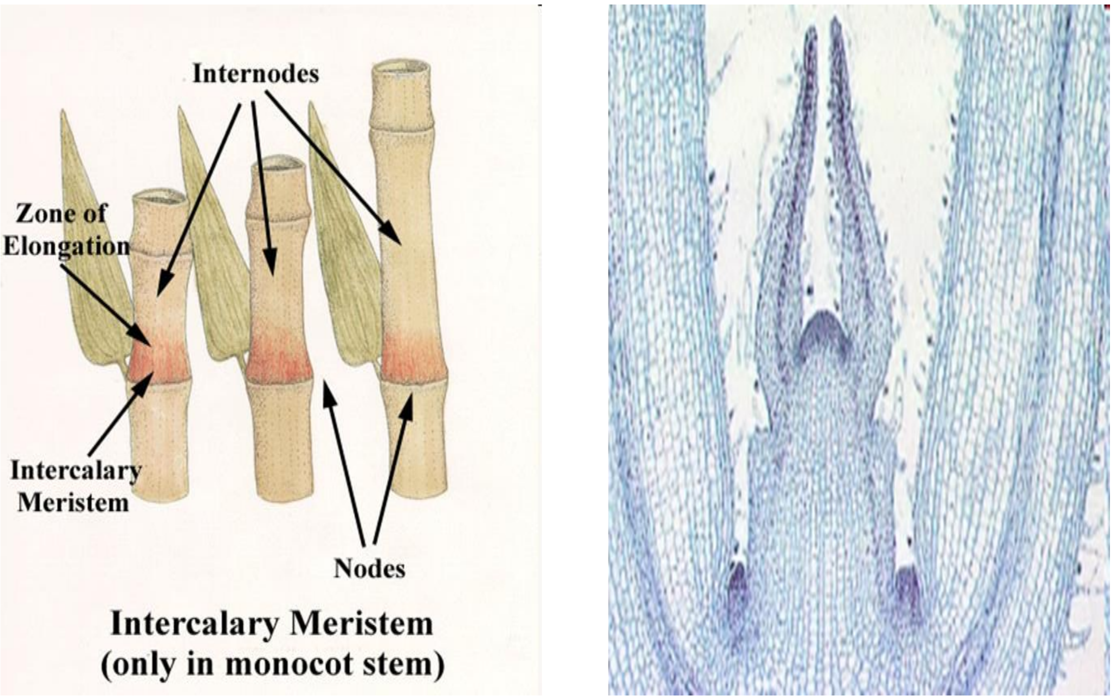


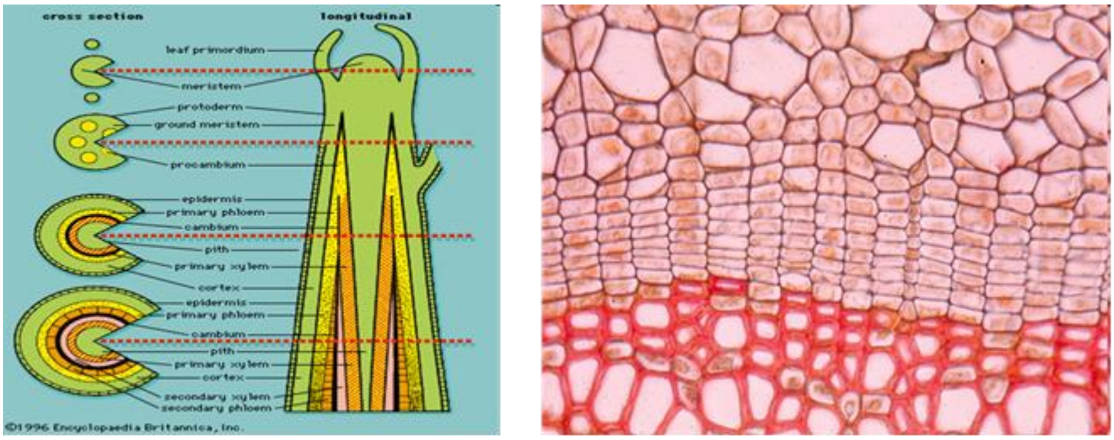
Fig. L.S of shoot - showing the positions of meristem



Apical meristems



Intercalary meristems



©1996 Encyclopaedia Britannica, Inc.

Lateral meristems

5- <u>Meristems based on function:</u>

Protoderm: The meristematic region which gives rise to the epidermis.

Procambial strands: The meristematic region which gives rise to the vascular tissue.

Ground meristem: The meristematic regions which give rise to the cortex, pericycle, medullary rays and pith.

There is also another old classification which statesينص على that primary meristem could be divided into three regions, these are:

Protoderm: (dermatogen) which gives rise to the epidermis.

Periblem: which give rise to the cortex.

Plerome: gives rise to the central part of the axis (stele, pith and medullary ray).

Theories of structural development and differentiation

A- Shoot apex:

Various theories have been formed to describe the structure of the shoot apex of which are:

(1) **Apical cell theory:** The simplest special meristem is that which have a single large initial cell at the apex of the promeristem. Its shape is often pyramidal, and its derivatives show special arrangement indicating an alternating division along the faces of the apical cell. Promeristems with apical cell occur in lower vascular plants and are not known in seed plants.

(2) The histogen theory: This theory was developed by Hanstein (1970), it states that the apical meristem is characterized into definite meristematic regions responsible for building definite regions of the 1ry body of the stem (these meristematic regions are called histogens or tissue builders). These histogens are 1- the **dermatogen** which is the external layer responsible for building up the epidermis 2- the **Periblem**, which give rise to the cortex and the **plerome**, which gives rise to the central part of the axis.

Objections against this theory are:

a- These regions or histogens are not clear in many stems of higher vascular plants.

b- It does not have any morphological significance, which mean that, there is no definite specialization in function of these regions.

3- The tunica corpus theory: This theory was developed by Schmidit and Foster (1924), it says that apical meristem may be distinguished into two regions, 1- a central region with large cells which divide in several planes parallel and perpendicular to the surface and results in increase in mass. This region is called **the corpus**. 2-The other enveloping region which consists of one or more peripheral layers of smaller cells that divide only in one plane (at right angle to the surface) resulting in increase in area. This region is called **the tunica**. The tunica gives rise to the epidermis and several layers of the cortex while the corpus gives rise to the inner portion of the cortex and the central region of the axis.

B- Root apex:

The apical meristematic region in the root is shorter than the stem. The Hanstein's histogen theory is more applicable than in case of the stem and the histogens are more obvious. Each meristematic region has its origin in a group of initials and the large plant groups differ according to the origin of the different zones.

1- Root apex of pteridophytes:

Here there is a single apical cell and the structure of the root apex is the same as that of the stems of these plants.

2- Root apex of gymnosperms:

The majority of these plants have two groups of initials; the inner one forms the plerome whereas, the outer forms the periblem and the cap. The dermatagen is formed from the periblem.

3- Root apex of angiosperms:

There are three or four groups of initials:

a- In dicots: The outer initial forms the cap and the dermatogen, the median forms the periblem and the inner forms the plerome. The most important characteristic is the common origin of cap and dermatogen.

b- In monocots: Like the dicots except that the outer most layer forms the cap only, the next forms the dermatogen and periblem. Independence of origin of cap and dermatogen is therefore characteristic of these plants.

c- In aquatic monocots: Rarely there are four groups of initials, the outer layer of initials is the calyptrogen which gives rise to the root cap, next to it the initial gives rise to the dermatogen, and inner to it the initial gives rise to the periblem and the most inner gives rise to the plerome.

PERMANENT TISSUES AND THE TISSUE SYSTEMS

1- According to the stage of development:

Meristematic and permanent tissues: Meristematic tissues are immature tissues in which growth is taking place, while permanent tissues are those in which growth has ceased at least temporarily.

2- According to the kind of constituent cells:

a) Simple and complex tissues: Simple tissue is the one which is composed of a single type of cells forming a homogeneous or uniform mass while complex tissue is a heterogeneous tissue formed of more than one kind of cells working together as a unit.

Example of simple tissues are: **parenchyma, collenchyma, and sclerenchyma.**

Example of compound tissues are: **xylem** and **phloem.**

b) Tissue system: Certain cells dispersed among other tissues and performing certain function, example is the **secretory tissue system.**

PARENCHYMA

The parenchyma tissue is the least specialized permanent tissue in the plant body. It is the main constituent of the ground tissue and may be found in all plant organs as a continuous tissue as for example in cortex and pith of stems, cortex of roots, and mesophyll of leaves. Parenchyma cells are also components of certain complex tissues such as the xylem and phloem.

Parenchyma cells are potentially meristematic, i.e. they have the capability of being reverted to meristematic cells. Phylogenetically, parenchyma is considered a primitive tissue for the following reasons:

1- Being potentially meristematic.

2- They represent the origin from which other cells have evolved by specialization.

3- They are not functionally specialized.

Characters of Parenchyma cells:

1- Isodiametric in most of cases, other shapes are known.

2- Living cells, mostly with thin cellulosic walls.

3- Simple pits are mostly present in the walls.

4- Plastids may be present and large vacuoles.

5- Potentially meristematic.

6- Presence of large intercellular spaces.

Shape of cells:

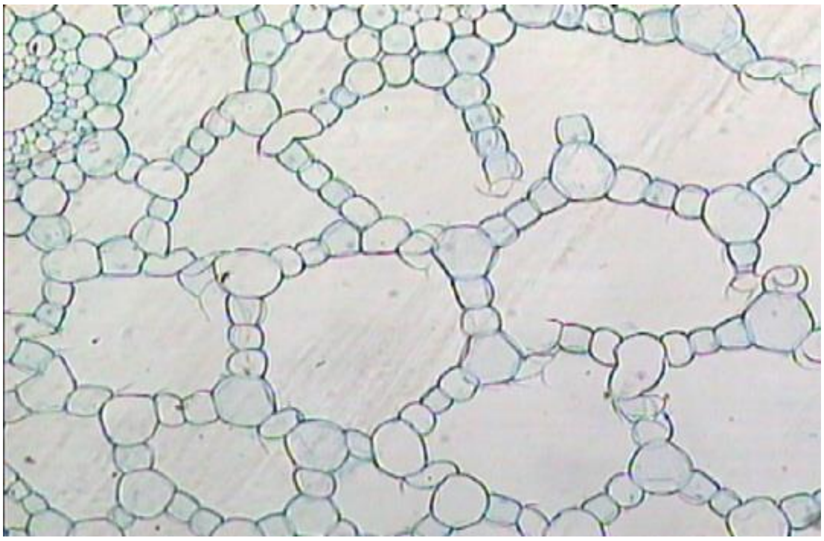
Parenchyma cells are usually isodiametric, although other shapes and types are common, the important types are:

(1) Spongy parenchyma: Cells are usually isodiametric, oval, spherical or irregular. This tissue is seen in leaves, cortex of herbaceous plants where there is an extensive air space system between the cells for gaseous exchange.

Spongy parenchyma

(2) Aerenchyma: This tissue is found in stems of aquatic plants where the cells enclose large intercellular spaces. These air spaces which serve for storage of gases for photosynthesis. The cells are mostly armed.

Aerenchyma

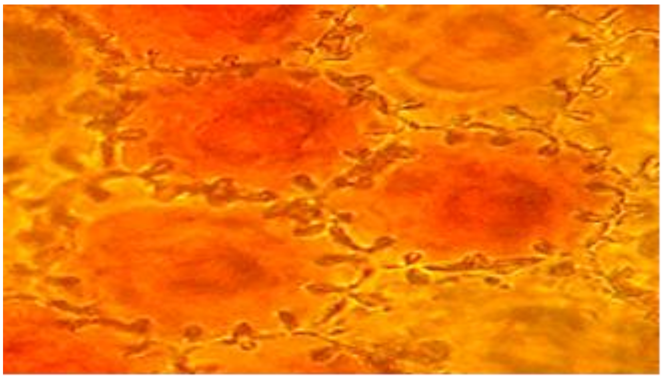


(3) **<u>Palisade parenchyma:</u>** The cells are elongated and cylindrical with their long axis at right angle to the surface of the organ. They are rich in chloroplasts which occupy peripheral position. They are found in leaves where there is usually one or two layers under the epidermis.

Palisade tissue

(4) **<u>Folded Parenchyma:</u>** Example of this tissue is found in **<u>Pinus</u>** leaf. The cells are provided with flanges projecting into the cavity of the cell providing extra wall surface area for the positioning of chloroplasts; and if flanges are hollow, they provide extra air space.

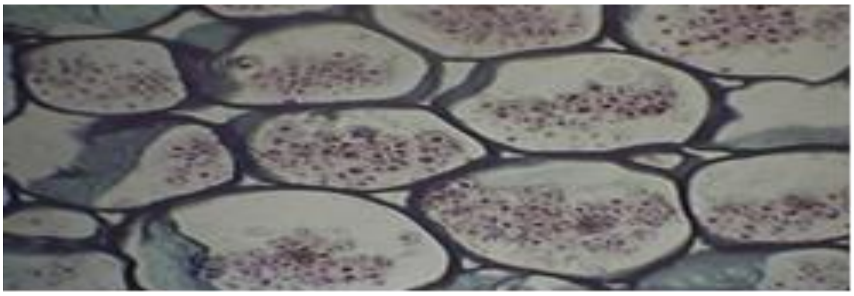
Folded Parenchyma



(5) Food-storage parenchyma: Food may be stored in the parenchyma cell sap in liquid or solid form. Parenchyma storing starch are common in storage organs. In some cases, as in the parenchyma cells of the endosperm of **Phoenix dactylifera** (date) food. Hemicellulose is stored in the primary walls which therefore appear very thick.

(6) Chlorenchyma: Isodiametric parenchyma which contain chloroplasts are common in cortex of stems of herbaceous plants, and leaf mesophyll.

Chlorenchyma



(7) Lignified Parenchyma: Parenchyma cells with lignified secondary walls are known. Cells are angular without intercellular spaces and mostly they are living. They function in support.

Cell wall:

The cell wall of parenchyma cell is often thin composed principally of cellulose, hemicellulose, and pectic substances. The cell wall arises during cell division at the early stage of telophase. At early telophase, the two daughter nuclei are connected to each other by the spindle fibers referred to as **phragmoplast**. In the equatorial plate, the cell plate is formed which contain pectic material which is then transferred to the middle lamella. Each of the two protoplasts of the two daughter cells lays down. Next to the middle lamella a wall containing cellulose, hemicellulose and pectic substances. The deposited wall is usually relatively thin in early stages of its development, but in latter stages it increases in thickness. A parenchyma cell may only develop a 1ry wall, however in some cases 2ry wall composed of lignin and cellulose is deposited (such as in lignified parenchyma). Parenchyma of cortex, pith and mesophyll have 1ry walls. **Pits:**

The walls of parenchyma cells have thin areas that constitute the pits. The pit in the primary wall develops as a depression referred to as the primary pit field. Further increase in thickness of the wall results in the formation of simple pit which is usually sharp and defined canal or cavity in the wall. The cavity is of the same diameter throughout the pit. Commonly a pit in the wall of one cell has a counterpart in the adjacent cell. The two pits are called pit pair. The two pits are separated by the pit membrane which is formed of middle lamella and two thin layers of the primary walls located at the bottom of the pit.

Plasmodesmata which are thin cytoplasmic strands connecting the protoplasts in the two adjacent cells usually penetrate the wall through the pits.

Contents:

The contents of parenchyma cells vary largely in relation to the metabolic activities of these cells. Some of the common components are:

(1) Plastids: Chloroplasts occur in the cells of leaf mesophyll and are absent in the cells of the underground parts. In serial parts cells with chloroplasts are usually present in layers near the surface of the organ. Parenchyma cells containing chloroplasts are called Chlorenchyma.

The chloroplast appears under the electron microscope composed of a colorless protein matrix called the **stroma** in which the chlorophyll bearing units which are called the **grana** are embedded. The plastid is surrounded by a semipermeable membrane. Each granum consists of several discs arranged above each other so that the granum has the shape of a short cylinder. Fine membranes connect one granum to another.

The chloroplasts develop from simple proplastids present in the meristematic cells.

Plastids that have no color are the **leucoplasts**. Upon exposure to light, they may develop chlorophyll. There seems to be a relation between chloroplasts and leucoplasts since grana occur also in the leucoplasts. Leucoplasts are usually the centers of starch storage and are referred to as amyloplasts, others may store fats and are called elaioplasts.

Plastids containing coloring substances other than chlorophyll are the **chromoplasts**. Examples are those containing carotenoid pigments and have yellow, orange, or red color. They are found in petals of many flowers and in various fruits. Grana is also found in chromoplasts of some plants. The chromoplasts vary in shape but are chiefly irregular, granular, spiral, angular, acicular, or forked they resemble crystals. It is sometimes considered that such shapes are due to the presence of pigments in crystalline form. In young carrot and tomato cells, the chromoplasts have the shape of ordinary plastids.

(2) Mitochondria: Also called chondriosomes, are small cytoplasmic bodies. They are difficult to separate from proplastids and other small bodies such as the lipoidal granules. They may be spherical, or rod shaped and are composed mainly of proteins and lipids. Each have a double membrane; the inner is folded in the interior. They are difficult to see by the light microscope and are easily seen by the electron microscope Mitochondria are physiologically important especially in respiratory mechanism.

(3) Ergastic substances: They are nonprotoplasmic components they are waste products that result from cellular activities or represent storage food substances. One of the most important is starch which develops in the form of grains in the plastids. Storage starch is formed by leucoplasts. An emyloplast may contain one or more starch grains.

Starch grains vary in shape and commonly show layering centered around the hilum that may be in the center or to one side. Splits that sometimes radiate from the hilum may result from dehydration of the grains. Layering or stratification may be due to an alternation of starch-rich and water rich layers. Others consider it to be due to an alternation of two carbohydrates: amylase and amylopectin. The amylose is more soluble in water than the amylopectin and when the grain is placed in water the differential swelling of the two substances causes the layering.

Storage starch occurs in the parenchyma of the cortex and pith, in parenchyma cells in the vascular tissues, and in parenchyma of fleshy leaves (bulb scales), rhizomes, tubers, fruits, cotyledons and the endosperm of seeds.

Another group of ergastic substances are the **tannins** which occur in the cytoplasm, the vacuole and impregnate the walls. They are abundant in leaves of many plants, in vascular tissues, in the periderm, in unripe fruits, in seed coats.

Crystals are also important and found in various shapes they are composed of calcium oxalate. Examples are, the solitary types, the raphides and the druses.

Solid protein may be present as ergastic substance in the form of amorphous **aleurone** grains, found in the endosperm and embryo of many seeds, and in the form of protein crystalloids.

Fats and related substances occur as ergastic substances. They occur in plastids or cytoplasm. Fats are reserve materials in seeds, spores, embryos and meristematic cells. They may occur as solid bodies or as droplets.

Function: Parenchyma serves various functions in the plant body. Cells may serve for food storage, food assimilation, aeration, or support. Support is performed by lignified parenchyma and thin-walled parenchyma may give some amount of rigidity to the plant body due to their turgor. Conduction, absorption, and protection are also other functions of certain types of parenchyma. Parenchyma cells may be transformed to the meristematic condition and divide.

COLLENCHYMA

Collenchyma is a simple living tissue which functions mainly in support. The most important characters of collenchyma cells are:

1- Early development from meristematic cells.

2- Adaptability to change in the rapidly growing organs especially those that increase in length.

3- Elongate cells.

4- Unevenly thickened primary walls which is composed of cellulose and pectic compounds.

5- High water content of the walls.

6- Living cells, they contain protoplast.

7- Intercellular spaces are rare, or completely absent.

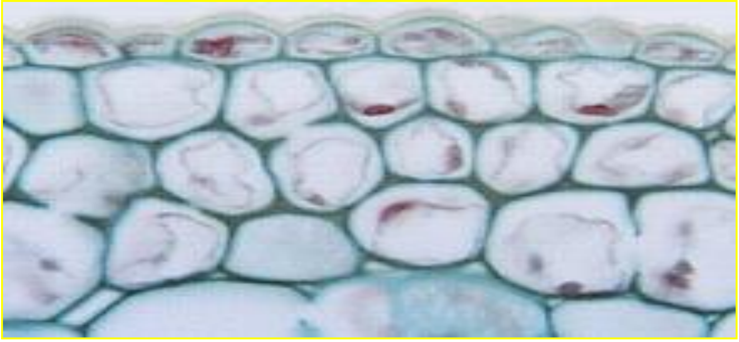
The cell wall:

Walls are thick, they contain cellulose, pectic substances but no lignin. Since the pectic substances are hydrophilic, collenchyma walls are rich in water. By treating cells with alcohol (dehydrating agent) cell wall contraction occurs.

The walls are plastic i.e., extensible and adapted to rapid growth. Therefore, collenchyma cells are suitable for support of rapidly growing organs.

The distribution of the wall thickening in collenchyma shows several patterns. Thickening is sometimes localized at the corners of the cells; such type of collenchyma is called **angular** **Cucurbita pepo** stem. Sometimes thickening is more on the tangential walls and collenchyma is called **Lamellar or plate** collenchyma as in the cortex of **Sambucus nigra** stem.

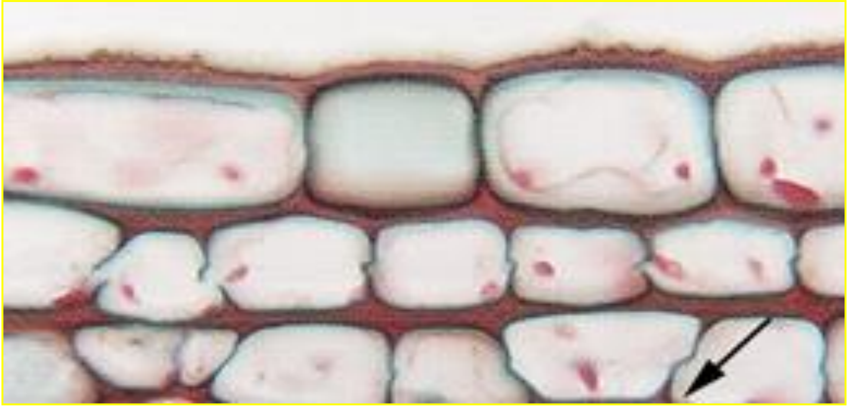
Angular Collenchyma



Collenchyma may or may not enclose intercellular spaces. If spaces are present in the angular type, the thickened walls occur next to the intercellular spaces. Collenchyma with such character is called **lacunar** or **tubular,** collenchyma as in the cortex of ***Lactuca*** petiole.

The three types of collenchyma are probably related to cell arrangement. Where the cells are irregularly arranged, the 1st type occur, where the cells lie in tangential rows, the second type occur, where intercellular spaces are present, the third type is formed.

Wall thickening appear early in the development of the cells while increase in cell size is taking place, therefore increase in length and size occur at the same time.



Lamellar Collenchyma

Shape: Cells are elongate in L.S. and rounded, angular, oval or irregular in T.S. The cytoplasm is prominent and may contain chloroplast although photosynthesis is not a function of collenchyma. Intercellular spaces occur only in lacunar type.

Development:

Collenchyma develops from elongate meristematic cells that appear very early in the differentiating meristem.

Pits: Occur in the wall of collenchyma and are mostly of the simple type.

Distribution:

Collenchyma occurs chiefly in the outer parts of stems, petioles, and leaf midribs. Its supporting value is increased by its peripheral position where it is located either directly below the epidermis or one or few layers from it. In stems, collenchyma frequently forms a continuous layer around the circumference of the axis, sometimes it occurs in strands at the ridges or angles of the organ. In the leaf blade it occurs in the ribs accompanying the larger vascular bundles, sometimes on both sides of the rib and sometimes on the lower side only.

The stems of typical woody plants rarely possess collenchyma, stems of monocot and roots are in general without collenchyma.

Structure in relation to function:

Collenchyma is particularly adapted for support of growing leaves and stems. Its wall being to thicken early during the development of the shoot, but this thickening is plastic and capable of extension. It therefore does not prevent elongation of the stem and leaf. In herbaceous stems which does not develop sclerenchyma, collenchyma is the main supporting tissue.

In stems with secondary thickening the xylem becomes the chief supporting tissue together with the sclerenchyma, therefore the role of collenchyma as supporting tissue is not important in woody plants.

SCLERENCHYMA

The cells of this tissue in contrast with those of collenchyma have hard, usually lignified walls with low water content. At maturity they usually have no protoplast. The walls are uniformly and strongly thickened. The thick wall of the sclerenchyma is suitable for studying the wall structure and development.

When a secondary wall is present the following layers are found:

a) middle lamella composed of pectic compounds.

b) 1ry wall composed mainly of cellulose accompanied by no cellulosic substances such as hemicellulose and pectic compounds.

c) 2ry wall composed mainly of cellulose accompanied by various no cellulosic substance but no pectic compounds, lignin may be present. In cells with 2ry wall, the 1ry wall is thin and finally united with the middle lamella.

Sclerenchyma cells when mature have thick lignified secondary walls and no living contents. Due to their thick nonplastic walls they cannot stretch so they do not mature until the plant organ ceases to elongate. Their main function is support and they vary greatly in shape. Based on the size and shape of the cells, sclerenchyma is classified into two main groups.

1- Fibers, 2- Sclereids.

FIBRES

Fibres are elongate sclerenchyma cells, usually with pointed ends. Chemically, the walls are usually lignified, although there are fibres with walls composed largely of cellulose. The pits of fibres are always small and round. In mature cells the pits are functionless unless protoplast is present. The lumen of the fiber is small and represents a small channel in the cell which may be blocked at certain places. In some fibers no lumen is present. In most kinds of fibres the protoplast disappears as the cells reach maturity and the cell is dead and empty. Fibres that retain their protoplasts also are present and occur in xylem of some plants.

Classification of fibers:

Fibers occur in nearly all parts of the plant. They are mostly found in the cortex. pericycle, phloem and xylem. Morphologically there are two types of fibers. The fibers of the cortex, pericycle and phloem possess simple pits and are therefore different from those of the xylem which have bordered pits.

Fibers are therefore two types: (1) bast fibers (2) wood fibers.

1- Bast Fibers: Include fibers of the cortex and pericycle as well as the phloem. Fibers are best to be termed by the tissue in which they occur as cortical fibers, pericyclic fibers, phloem fibers and wood fibers.

Fibers occur in small groups scattered among other cells. Usually, they form strands of tissue extending longtudinally for some distance. Their value as strengthening tissue is due to their arrangement in long masses and to the overlapping and interlocking of the cells.

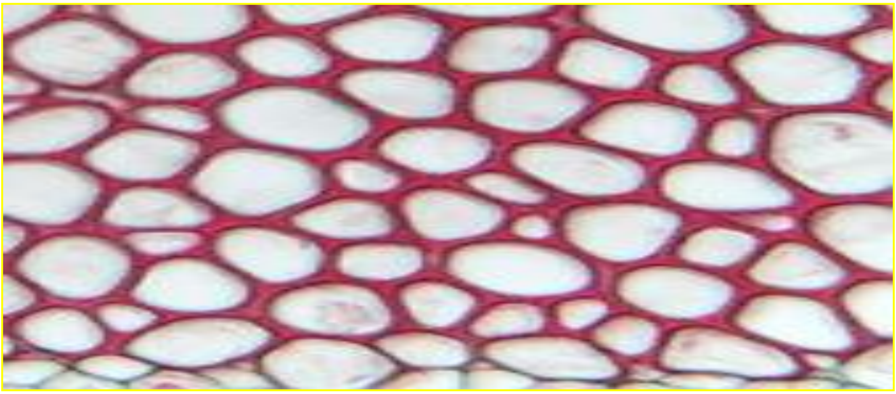
Fibers develop in two ways. In the fibers which are few mm long, all parts of the cell are always at the same stage of development at the same time. In long fibers as those of **flax** the cell elongates apically and the 2ry wall develops in part of the cell while the apex is still growing.

Occurrence:

In the dicots, fibers are particularly common in the vascular tissues. In monocots, fibers may completely enclose each vascular bundle forming a bundle sheath or form layers away from the vascular tissues.

Phloem fibers occur in many stems. Usually, they originate in the 1ry phloem, but matures after this part of the phloem is functionless. Therefore, they are called 1ry phloem fibers. Phloem fibers are of common occurrence in the stems of ***Tilia, Sambucus, Clerodendron, vitis, flax.***

Conifers may have 2ry phloem fibers. fibers that originate on the periphery of the vascular bundles but do not originate from the 1ry phloem are referred to as perivascular fibers or pericycle fibers.



Fibers

SCLEREIDS

The sclerids are widely distributed in the plant body and vary in shape. These cells have very thick 2ry wall, strongly lignified and usually isodiametric. The pits are very small, with round aperture and their cavities often form branching canals due to the union of the pits together.

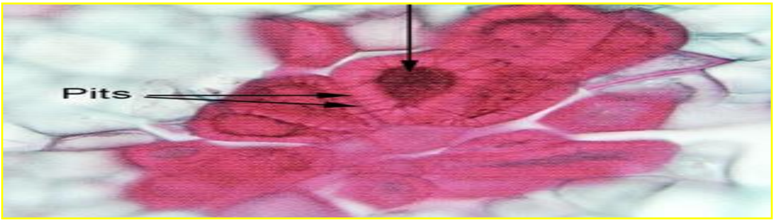
Sclereids occur anywhere in the plant body, mostly they occur in the cortex, in the phloem and in fruits and seeds. They occur singly or in group. When sclereids, are scattered they give hardness to the organ as in leaves and the flesh of fruits. When they are present in masses they give hardness and mechanical protection as in the seed coats and nut shells.

Sclereids vary greatly in shape. The simple type of sclereid resembling a parenchyma cell in shape is called a stone cell or ***brachysclereid*** such as these present in some types of stems and in the fruit of pear.

Elongated sclerides called ***macrosclereide*** are collumar in shape such as those constituting the epidermal layer of many seed coats of leguminous seeds such as in ***Pisum sativum*** (pea) seed coat.

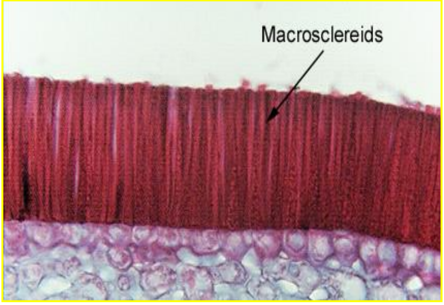
Osteosclereids (bone cells) are bone like or barrel shape with rounded ends constitute the hypodermal layers in many seed coats as peas and beans and in the mesophyll of ***Hakea*** leaves.

Astrosclereids are lobed or armed or star shaped with arms radiating in all directions. They are present in leaves and stems of aquatic plants as ***Mymphea*** petiole where the arms project into the air cavities preventing blockage by water and providing local support. ***Filiform sclereids*** or ***Trichosclereids*** occur in leaves of some xerophytic plants and can be shown in ***Olea*** leaf.



Stone cells

Osteosclereids



Astroscleride

XYLEM

The xylem is the principal water conducting tissue of a vascular plant. It is usually associated with the phloem (the food conducting tissue). The two tissues together are called the vascular tissue system.

Developmentally, it is convenient to distinguish between primary and secondary vascular tissues. The primary tissues differentiate during the formation of the primary plant body which is maintained through the activity of the apical meristem. The meristem which is directly concerned with the formation of the primary vascular tissue is the procambium or called the perivascular tissue.

The secondary vascular tissues are produced during the second major stage of plant development, in which an increase in thickness results from lateral additions of new cells to the primary body. It results from the activity of the vascular cambium. The primary and secondary xylem have histologically differences, but both are complex tissues containing water conducting elements, parenchyma cells, fibers and other types of cells.

Types of Cells:

Tracheids: The fundamental cell type in xylem is the tracheid. The tracheid is an elongated cell with tapering ends which when mature is nonliving, i.e., without protoplast. The walls are hard, relatively thick and are usually lignified. In cross section, the tracheid is typically angular. The ends of the tracheid do not taper uniformly, but tapering is confined to one side of the cell only. Tapering is seen in tangential sections of the tracheid, whereas radial sections do not show tapering and the end of the cell in such sections is somewhat rounded. The pits are abundant in the cell wall and are usually of the bordered type. The lumen of the tracheid is large and free of contents of any kind.

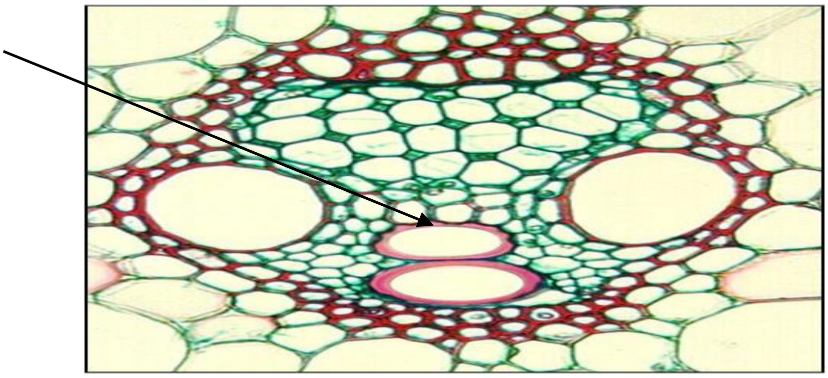
The tracheid is well adapted structurally to its function which is water conduction primarily and support secondarily. It is a long empty, hard walled tube extending parallel with the long axis of the organ. It is in communication with neighboring tracheids as well as other cells by means of pits which permits diffusion into adjacent cells. Therefore, tracheids make channels for longitudinal conduction. Tracheids are mainly characteristic of the gymnosperms and are the primitive type of cells of xylem.

Pits of tracheid walls:

The position of pits in the wall of the tracheid and the size and shape of pits depend upon the position and nature of the adjacent cells. The various larger plant groups have constant types of bordered pits which have characteristic shape, torus, and extent of border. The ferns have transversely elongated pits, with narrow border and little or no torus. The pits lie close together covering the wall giving it a ladder like appearance and the cells are called ***Sclariform tracheids.***

In gymnosperms, and most angiosperms, the bordered pits are chiefly rounded with borders. The best development of the torus is in the gymnosperms where the bordered pits are highly developed. The pit membrane can easily change its position from a median position to a lateral one, therefore, the torus can tightly close the aperture. In this way, the torus is acting like a valve and the pit is open when the torus is in a median position and closes when it moves to a lateral position. This system is characteristic of water conducting cells. Other cells provided with bordered pits, but are not active in conduction, their bordered pit membranes have lost the capacity for movement.

tracheids

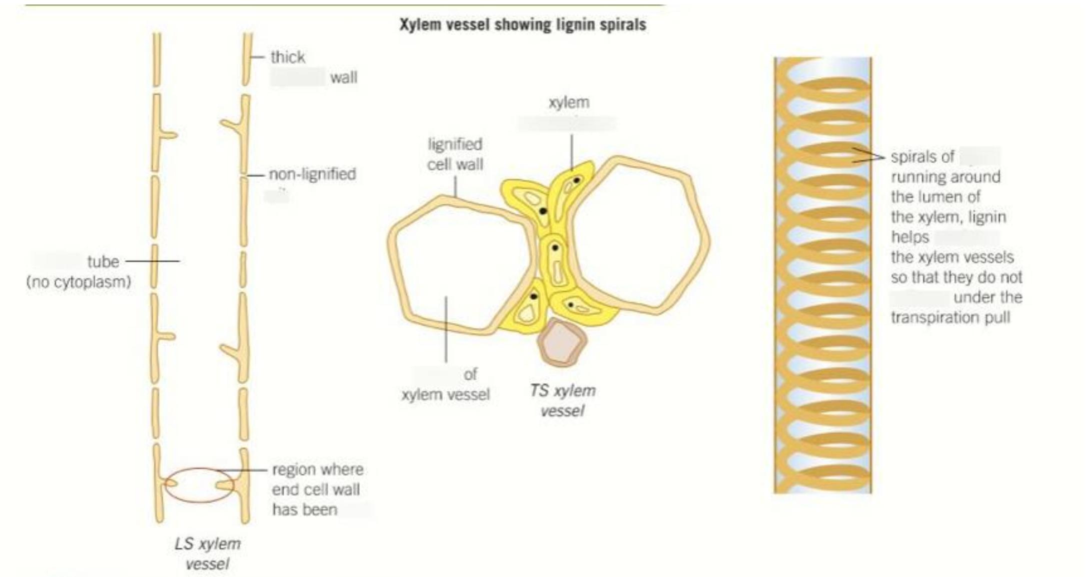


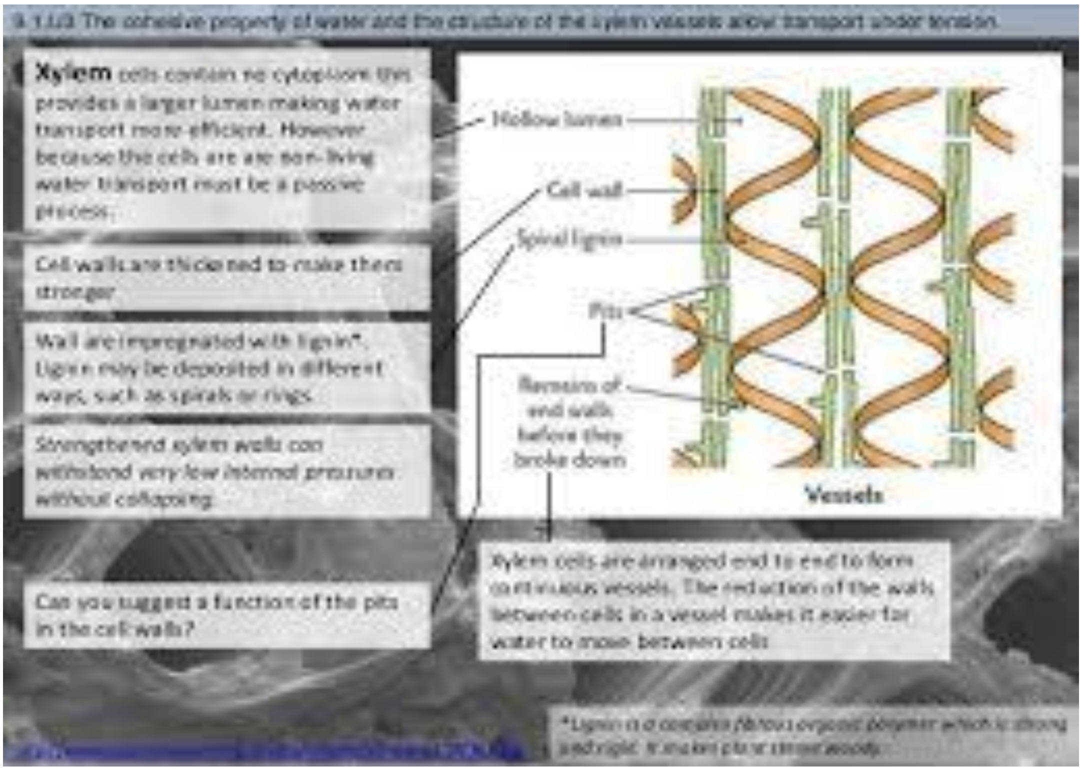
Function of the tracheid:

The tracheid is adapted structurally to the function of conduction due to the large lumen and the hard wall which permits passage of water and dissolved minerals against gravity under the influence of root pressure. The thick wall of the tracheid makes it suitable to aid in support. The overlapping and interlocking of the cells to form strands is also important in supporting function. It is noticed that where fibers are absent, tracheids play the important role in support. In evolutionary development, segregation of function takes place and more specialization in function is characteristic. In the xylem tissue, the fibers are specialized in support and the vessels in conduction.

Vessels:

The term vessel is used for the series of conducting cells which are placed in a definite tube-like system with perforations at the end walls and providing conduction in straight line, the term tracheas is also used. In the evolutionary development of the trachea, the diameter of the cell has increased, and the end walls have become perforated by large openings. This specialization permits direct transport of water from cell to cell. The more primitive types of vessels have the shape of tracheids with relatively small lumen. In advanced vessels, the diameter of the lumen is large. The ends of the cells also change in shape. In the evolution of the tracheid, the angle made by the tapering ends becomes greater and greater until the end walls are at right angles to the side walls. Intermediate forms of vessels with tapered end walls are known. In vessels wall thickness is almost the same as the tracheids, although there are vessels with thicker walls. The pits are often more numerous and smaller than those of the tracheids. When pits are abundant, they may be scattered or arranged in a definite pattern depending on the type of the neighboring cell. When the neighboring cell is a vessel, pits are numerous, while they are few if the neighboring cell is a fiber.





9.1.U3 The cohesive property of water and the structure of the xylem vessels allow transport under tension.

Xylem cells contain no cytoplasm this provides a larger lumen making water transport more efficient. However because the cells are are non-living water transport must be a passive process.

Cell walls are thickened to make them stronger.

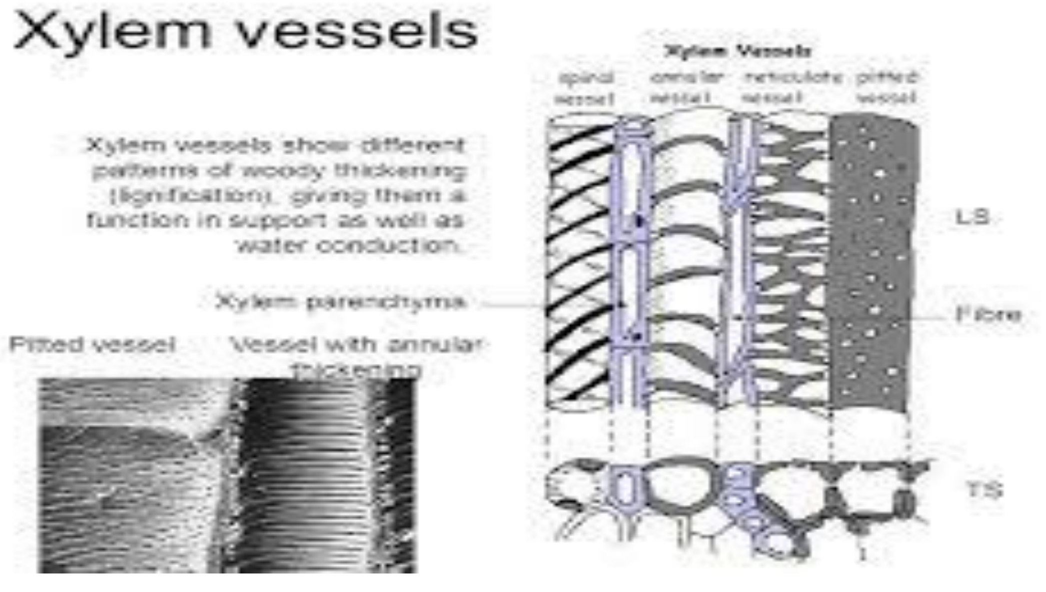
Wall are impregnated with lignin*. Lignin may be deposited in different ways, such as spirals or rings.

Strengthened xylem walls can withstand very low internal pressures without collapsing.

Can you suggest a function of the pits in the cell walls?

Xylem cells are arranged end to end to form continuous vessels. The reduction of the walls between cells in a vessel makes it easier for water to move between cells

*Lignin is a complex fibrous organic polymer which is strong and rigid. It makes plant stems woody.



Xylem vessels

Xylem vessels show different patterns of woody thickening (lignification), giving them a function in support as well as water conduction.

Types of Perforations:

Openings in vessel element walls known as perforations are mainly present in the end walls and in rare cases in which the end walls are tapering, they are present in the side walls. Perforations in vessel occur at each end of the element. The area of the wall in which perforation occurs is the perforation plate-end wall. The portion of the plate remaining after perforation is the perforation rim, the strips of walls remaining after perforation are the perforation bars.

Perforation plates may be simple, if there is only one opening, if there are two or more openings it is called multiple. Multiple perforations may be scalariform if the openings are mesh-like structure. The common types are simple and scalariform. Commonly, end walls which are transverse have simple perforations whereas those which are oblique have scalariform perforations. The scalariform type is more primitive than the simple type.

Vessels are characteristic of the angiosperms. In many monocots, they are absent from the stems or leaves. They are present in some species of gymnosperms. Vessels are more advanced than tracheids.

Development of the Vessel:

Vessels are formed from series of xylem mother cells (meristematic cells) by the fusion of the cells end to end during the last stage of development. This fusion involves the loss of the end walls or parts of it so that the lumen of the cells is open into one another forming a tube. The vessel element enlarges rapidly, increasing in diameter. During the rapid growth in cell size, the primary cell wall remains constant in thickness except at the end walls which disintegrates. During the enlargement of the cell, the cytoplasm remains active and at maturity it begins to disintegrate. After the primary wall is mature, the secondary wall is formed, and the perforation of the end walls and disintegration of the cytoplasm begins. The mature vessel is finally formed.

Xylem fibers:

A second evolutionary derivative of the tracheid is the wood fiber in which all the supportive features of the tracheid have been intensified. In the evolutionary development of the tracheid, the thickness of the wall has been increased and the diameter of the lumen has decreased, and the number and size of pits have been reduced. The wood fiber is longer than the tracheied and slenderer and tapering.

It has greater overlapping, more extensive and heavier wall thickening and lignification. Pits are reduced in number and size or are completely lost. Thus, the two derivatives of the tracheid, the vessel element and the wood fiber are complementary and together perform the dual functions of the original tracheid. Vessels and wood fibers together occupy, in function and position, the same place in the most highly evolved vascular plants that the tracheids do in the lower vascular plants.

Two types of xylem fibers are known, these are the fiber tracheids and the libriform fibers.

Fiber tracheids:

Between the typical tracheids and the fiber there are intermediate types which are not either fibers or tracheids and are called fibertracheid. The fibertracheid has bordered pits with cavities smaller than that of the tracheid or vessel. These pits also have a distinct pit canal leading from the pit cavity into the cell lumen through the thick wall. The aperture from the cell lumen into the pit canal (pit aperture) is elongated and may be slit like. It varies in length and may extend beyond the limits of the pit cavity. The aperture from the pit canal into the pit cavity (outer aperture) is circular. The canal has the shape of a funnel. The cell wall of the fiber tracheid is not very thick, and the cell lumen is intermediate in size between that of typical tracheid and a fiber.

Libriform Fibers:

This type of fibers is longer, and its wall is thicker than that of the fiber tracheids. They are called libriform wood fibers (liber=phloem) because they are like phloem fibers. The pit has a slit-like aperture towards the cell lumen, a canal like and flattened funnel but no pit cavity, i.e., the pit has no border, and it is a simple pit.

Septate fibers:

In fiber tracheid, the cell may retain protoplasts and the cell is separated by cross wall into a row of cells and is called septate fiber. They function in storage of food and therefore resemble wood parenchyma. Also, fiber-tracheids and libriform fibers may both be septate.

Gelatinous fibres:

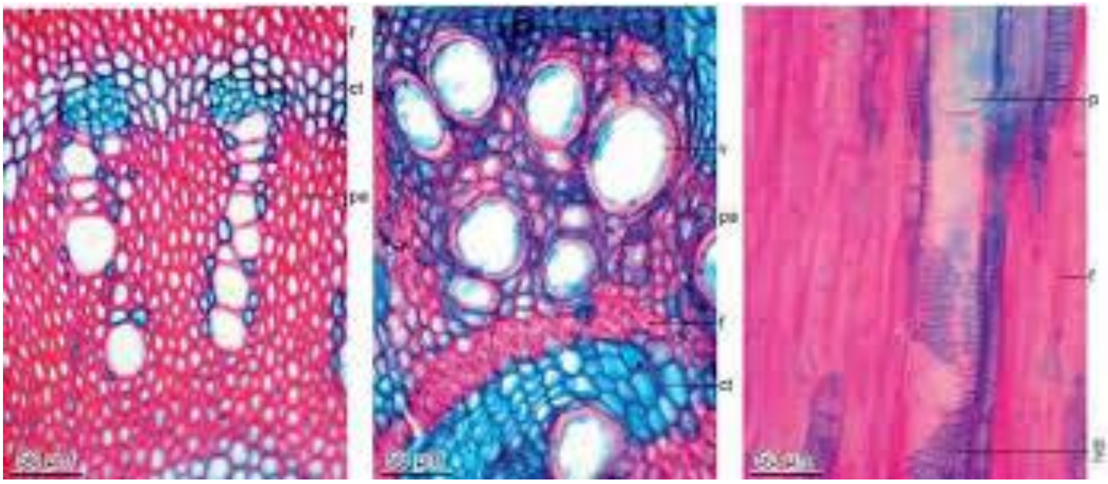
Gelatinous or cellulosic layers may occur in the wall of the fiber tracheide or libriform fiber, these are called gelatinous fibers.

Substitute fibers:

Parenchyma cells with fiber like form is called substitute wood fiber.

Wood parenchyma:

Parenchyma cells are a common constituent of the xylem of most plants. In secondary xylem they occur as vertical series of elongated cells placed end to end known as wood or xylem parenchyma, and radial transverse known as xylem-ray parenchyma. Both are alike in wall structure and contents. The parenchyma cell store starch, oils and many other ergastic substances. The walls may have secondary thickening and may be lignified. Some parenchyma cells may become sclerified by formation of thick walls forming sclereids. Parenchyma cells of xylem, unlike tracheids, vessels and most kinds of fibers, remain alive if the xylem is functioning.



PHLOEM

The phloem is the food conducting tissue of a vascular plant. Like the xylem it consists of several types of cells and could be classified developmentally into a 1ry and a 2ry tissue. The 1ry phloem develop from the procambium. The 2ry phloem is formed from the vascular cambium.

Cell types:

In xylem the fundamental structural and functional cell type is the tracheid; similarly, in phloem the basic cell type is the sieve element. There are two forms of the sieve elements which are the sieve cells and sieve tubes.

Phloem, like the xylem is a complex tissue, it may consist of:

a- Sieve cells and phloem parenchyma only as in the pteridophytes and many gymnosperms.

b- Sieve cells, parenchyma, and phloem fibers as in some gymnosperms.

c- Sieve tubes, companion cells, phloem parenchyma, phloem fibers and sclereids as in angiosperms.

The sieve cells and sieve tube elements:

Both are alike in their fundamental structure and function. They both are elongate living cells with a thin cellulose wall. The protoplast has a large central vacuole and a thin peripheral layer of cytoplasm. No nucleus is present when the cell is mature. The cytoplasm contains leucoplasts which in some plants store starch. The walls are of the primary type. Sieve cells, and sieve tubes differ in the following:

1- The degree of specialization of the sieve areas and differences in their distribution on the walls.

a- In sieve cells the sieve areas are not highly specialized and are not aggregated on special wall parts into sieve plates.

b- In sieve tube element, the sieve areas are aggregated in special parts of the wall, the sieve plates, usually at ends of the cells.

2- The sieve tubes elements form vertical series of cells which are connected through the sieve plates, forming sieve tube, whereas the sieve cell is formed of only one cell.

Sieve areas:

The sieve areas are wall areas with pores penetrated by cytoplasmic strands that connect the protoplast of adjoining cells. In lower vascular plants and gymnosperms, the strands are thin and uniform in size. In angiosperms, the size of the pores and the thickness of the strands vary considerably. Sieve areas with the larger pores and strands usually occur on the end walls. The wall parts with large pores and large connecting strands are called sieve plates (perforation plate of vessel). Each connecting strand is surrounded by callose, which is a carbohydrate which stains blue with aniline blue. Callose forms first a thin layer around a strand but accumulates as the sieve element gets older and close the element.

Two types of sieve plates are known:

1- Simple sieve plate with one sieve area.

2- Compound sieve plate with several sieve areas.

In the first type the plate occupies all the end wall which is commonly transverse, whereas in the compound type it occupies only part of the end wall which is usually oblique.

The sieve areas are scattered over the side and end walls. The number of sieve areas on the side walls varies greatly. There are usually few or none of sieve areas on the side walls where the end walls are transverse, but they are many where the end walls of the cells are tapering. Where sieve areas are lacking on the side walls, vestigial sieve areas, known as lattices, are often present.

In evolutionary development increasing of specialization is characterized by a decrease in the inclination of the end walls, reduction in the number of sieve areas on side walls, increase in the thickness of strands in the sieve plate. The most highly specialized sieve element has a simple sieve plate with large pores on end walls which are transverse and the sieve areas on the side wall are few and not specialized.

In the most primitive type, the ends are long tapering, and it is difficult to differentiate the end wall from the side wall. In more advanced types the end walls are oblique and in highly advanced types they are transverse. The primitive types of sieve tubes have many sieve areas whereas, the most advanced types have one area in a plate occupying nearly all the transverse end wall with few or no side walls.

Differentiation of the sieve tube member:

The sieve tube mother cell elongates, and the cytoplasm becomes highly vacuolated, the wall thickens, sieve areas develop in the end walls and the cytoplasmic strands become definite and callus develop around the strands. As the sieve element reaches maturity in size, the wall becomes thinner, the nucleus disintegrates, the connecting strands increase in diameter, the peripheral layer of the cytoplasm becomes thin and the sieve tube becomes functioning in conduction.

In all plants conduction by sieve tubes probably lasts only a short time from a few days to a year or more, then the callus increases in size and finally closing the element.

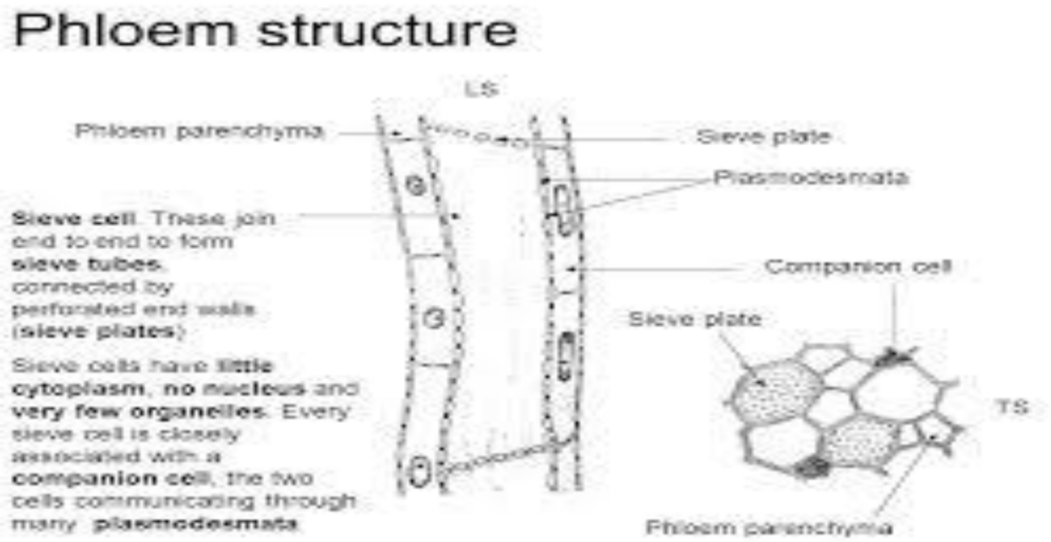
Companion cell:

It is a special type of parenchyma cell which is closely associated in origin, position, and function with the sieve tube elements. These cells occur only in angiosperms and they accompany the sieve tube elements. In monocots, they are abundant and with sieve tubes they make up the phloem.

Companion cells are formed by longitudinal division of the mother cell of the sieve-tube element before specialization of this cell begins. One daughter cell becomes a companion cell, and the other a sieve-tube element. Transverse division in the companion cell initial may form a row of companion cells. In a species the number of companion cells accompanying a sieve tube element is constant. Long solitary companion cells are common in primary phloem of herbaceous plants, short and numerous companion cells appear to be characteristic of the 2ry phloem of woody plants.

Companion cells have abundant cytoplasm and definite nucleus but do not contain starch. They live only so long as the sieve tube element with which it is associated is not crushed. In cross section it is triangular, rounded, or rectangular and small.

The presence of companion cells is usually associated with the presence of sieve plates in the sieve tube members. In Gymnosperms no companion cells are found, and certain cells called the **albuminous cells** are associated with the sieve cells they may be comparable to the companion cells.



Phloem structure

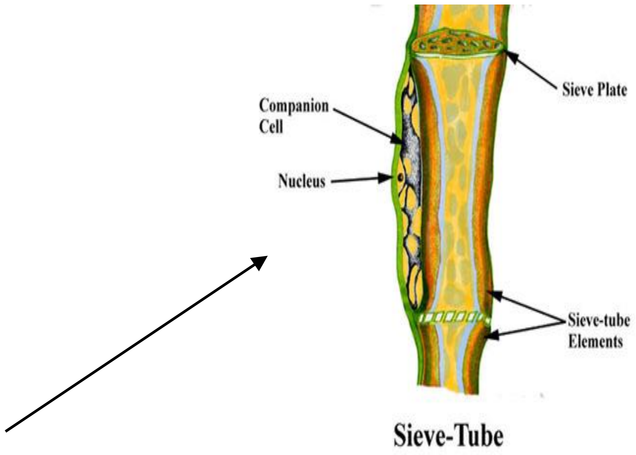
Sieve cell. These join end to end to form **sieve tubes**, connected by perforated end walls (**sieve plates**)

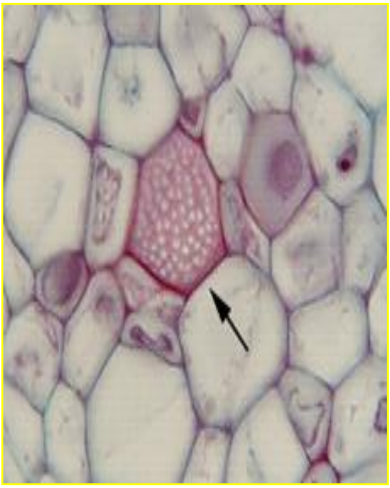
Sieve cells have **little cytoplasm**, **no nucleus** and **very few organelles**. Every sieve cell is closely associated with a **companion cell**, the two cells communicating through many **plasmodesmata**

Phloem parenchyma:

These cells range from elongate and tapering to cylindrical or spherical. The elongate cells may divide forming a row of cells. The cells may contain crystals, tannins, mucilage, latex or other substances. Most of the phloem parenchyma contain starch or oil.

Parenchyma may be lacking in the phloem of some plant groups as in phloem of the monocots which is composed of sieve tubes and companion cells only.





Sieve Plate

Phloem fibers:

Fibers are common components of both primary and secondary phloem. In the 1ry phloem, fibers occur in the outer most part of the tissue, while they are distributed in the 2ry phloem. The fibers may be nonseptate or septate and may be living or nonliving. They are long cells with thick walls and are the commercial source of fibers as in ***Linum*** (flax). Phloem fibers differ from xylem fibers in the form of pits. They usually have simple pits with round aperture. The walls may be lignified or composed mainly of cellulose as in flax. The 1ry phloem fibers are similar to those of the cortex and to those of the 2ry phloem.

Because of the strength of strands of phloem fibers, these have long been used in the manufacture of robes. Fibrous tissue used in these ways are known as **bast** and therefore, the term bast fibers is used for fibers other than wood fibers. Sclereids may be present in 1ry and 2ry phloem.

Function of phloem:

The chief function of the phloem is the conduction of food such as proteins and carbohydrates. The sieve elements are the cells concerned with conduction with the companion cells or albuminous cells. The fibers and sclereids serve for support and protection of these tissues. Many parenchyma cells are starch storage cells.

SECRETORY TISSUE SYSTEM

All cells that are directly concerned with the secretion of gums, resins, essential oils, nectar, and similar substances are referred to as secretory tissue. Such a classification is physiological and is based on function, it does not have any morphological significance. Secretory cells may be scattered in pith, xylem, phloem, cortex, or any region, or may be aggregated forming tissue in the morphological sense (ducts or glands). These may occur either as a single cell or in a mass and may be **external or internal** in position.

Secretory cells are often organized into special secreting structures commonly known as glands. Glands are of various function, they may secrete digestive enzymes and called digestive glands, and these which secrete nectar known as **nectarines** and these which secrete salts are **salt glands**. Other types are hydathodes, resin ducts, oil ducts, laticiferous ducts or glands. Glands or ducts may have central cavities where the secretion is stored. The cavities are either schizogenous like the resin ducts of ***Pinus*** or lysigenous like the essential oil glands of ***Citrus*** fruits.

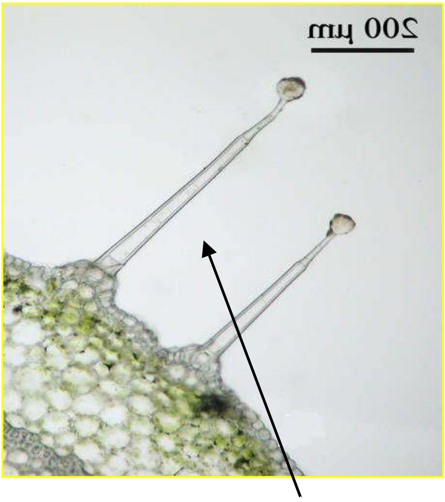
1- Digestive glands:

In insectivorous plants there are special glands which secrete protein digesting enzymes which digest the proteins of the insect. In ***Drosera,*** the secretory tissue is at the tips of the leaf hairs. They also secrete mucilagnous substances. Other examples are in ***Nepenthes*** and ***Dionea.***

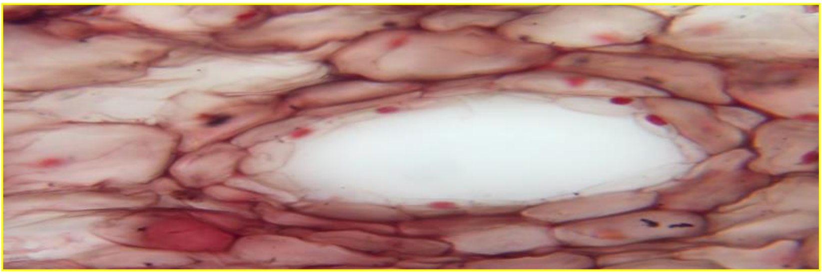
2- Nectaries:

Many plants produce nectar which attract insects. Usually, the secretion of nectar is from specialized epidermal cells which cover certain regions of the flower. In some nectaries the secreting cells are superficial upon the floor.

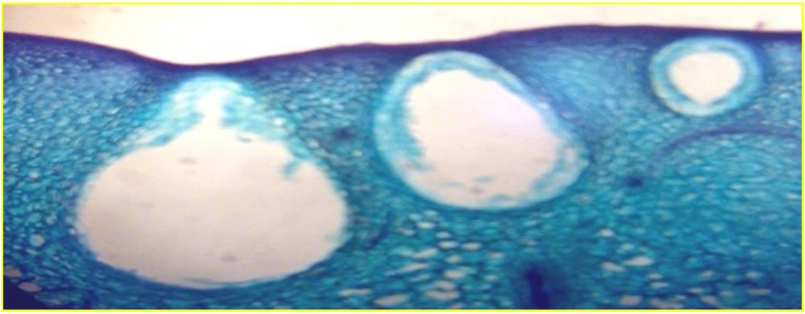
Digestive gland



Glandular hairs



Schizogenous gland



Lizogenous gland

3- Hydathodes

These are specialized water stomata through which water is released in the form of liquid. The phenomenon is called **guttation**, which is commonly found among plants inhabiting humid regions. The guttate liquid contains a mixture of various ions, sugars, amino acids, and other organic substances. Guttation is seen when root pressure increases due to availability of water and reduced transpiration under humid conditions.

4- Resin, oil and gum ducts:

In gymnosperms generally and in some angiosperms, resins, oils, gums, and other substances are secreted in ducts. In ***Pinus,*** these ducts may extend vertically through the plant. In some cases, they are short as in ***Umbilliferae.*** In ***Pinus*** the resin ducts are **schizogenous** and when mature they have the structure of a tube lined with epithelial cells. Those of ***Umbilliferae*** are like ***Pinus.*** The secretory cells lining these cavities are thin-walled parenchyma with dense protoplasm. Those of ***Citrus*** fruit rind are **lysigenous** cavities filled with essential oil and other substances and are formed by disintegration of the cells.

5- Laticiferous ducts:

Latex is found in several angiosperms. This substance is white, yellow, or reddish viscous fluid composed of proteins, sugars, gums, alkaloids, enzymes, and other substance such as starch grains. The latex of some plants is economically important such as those of ***Hevea*** source of rubber; papin from ***Carica;*** chicle from ***Achras.*** Laticiferous ducts are two types: latex cells and latex ducts.

a- Latex cells:

These are long cells extending for long distance through the plant. The cell contains many nuclei. Each arise from single meristematic cell which elongates and may branch. This type is found in the families, ***Asclepiadaceae, Apocynaceae,*** and ***Euphorbiaceae.***

b- Latex ducts:

They originate in the meristems from rows of cells. Therefore, they are resembling a xylem vessel in that it is made up of series of cells united to form a tube by the dissolution of end walls. Examples of this type are found in ***Papayeraceae, Caricaceae, Musaceae*** and ***Hevea.***

The functions of laticiferous tissues may be as following:

1- help in conduction of food substances.

2- store food materials of reserve mutrition.

3- regulate and maintain the water balance in the plant.

4- may work as agency for oxygen transport.

5- the most important function is to perform excretory roles.

THE PRIMARY PLANT BODY

THE PRIMARY VASCULAR TISSUE

The procambium:

The meristematic tissue which forms the primary xylem and phloem is known as the procambium. The first procambium appears as isolated strands very close to the apex in stem and root, commonly at only a few microns. The slender procambium strands increase in diameter by longitudinal cell division within themselves and by the addition of new cells upon their borders by transformation of adjacent meristematic cells. Increase in size of the strands may be so great that some or all the strands fuse and a hollow cylinder or a solid central core may be formed.

Differentiation of the procambium, (centripetal and centrifugal growth):

If the development of mature vascular cells from procambial strand progress from the point of beginning towards the center of the axis it is known as centripetal growth, and that away from the center of the axis is known as centrifugal growth. However, in centrifugal growth, the oldest structures are at the center and the youngest at the outside, and vice versa in centripetal growth. The development of the phloem is centripetal whereas, the xylem is centrifugal and sometimes centripetal.

In xylem, when the development is toward the center of the axis, centripetal xylem is formed, and the xylem unit is called exarch. When it is away from the center of the axis, centrifugal xylem is formed, and the xylem unit is end arch. When development is such that both centripetal and centrifugal xylem are formed, the xylem is mesarch. The terms centripetal growth and centrifugal growth refer to sequence of maturation of procambium cells in definite directions. The root is always exarch, the stem of seed plants is endarch, mesarch is common in ferns.

Protophloem and protoxylem:

The first cells of the phloem to mature are the protophloem, those of the xylem are the protoxylem. These cells differ from later formed cells of the same tissue in cell types, size, and shape. They are very slender and long because stretched since they are subject to stretching due to the rapid increase in length of the organ. The cells, to adapt this, are long and slender, with thin cellulosic walls, and in protoxylem they are provided with bands of lignified 2ry walls. These bands are in the form of rings, spirals. Therefore, such lignification keeping the shape of the cell.

The terms protoxylem and protophloem are restricted to these cells capable of stretching. The parts which are not stretched by elongation are known as metaxylem and metaphloem. The 1ry xylem is composed of protoxylem and metaxylem, but the 2ry xylem is not because secondary tissues develop only after elongation.

Primary Phloem:

The first vascular cells to mature in a given region are sieve elements of the phloem. There structure is difficult to determine because they closely resemble the procambium cells; they live for few days and are crushed. These cells are long because they are stretched. Later formed cells of metaphloem are shorter. The first protophloem consists only of sieve cells or sieve tubes distributed among procambium cells, companion cells are rare or absent. The metaphloem is a complex tissue with well-developed cells which are sieve cells or sieve tubes, companion cells, parenchyma cells and sclerenchyma in the form of fibers or sclereids. The various cell types are the same as those of 2ry phloem. The metaphloem may be crushed after formation of 2ry phloem. Therefore, it is of temporary function if 2ry thickening is to take place, but persist if no 2ry thickening occurs, such as in the case of monocots and some dicots as ***Cucurbita.***

Primary xylem:

Protoxylem is a complex tissue made up of tracheids, vessels and parenchyma cells. Fibers are probably absent. Thickening of the water conducting elements is made in such form to keep the element opened and permit stretching, it may be annular or spiral. The spiral thickening may take the form of a ladder due to the formation of bar like thickening running from corner to corner, this type is called scalariform. Metaxylem thickening is usually reticulate or pitted, these types are not capable of stretching. The scalariform type usually lie between protoxylem and metaxylem.

Protoxylem water conduction cells may be tracheids as in pteridophytes and gymnosperms or vessels as in angiosperms.

Protoxylem lacunae:

Where several protoxylem cells lying close together have been destroyed, a canal like cavity known as protoxylem lacunae is formed. It is of special occurrence in monocots and horsetails.

Types of Vascular Bundles:

A bundle consists of both xylem and phloem which both show several types of arrangement with each other in the bundles as follows:

1- Those in which the xylem and phloem lie radially side by side.

2- Those in which one type of tissue surrounds the other.

3- Those in which the two types are separated from one another.

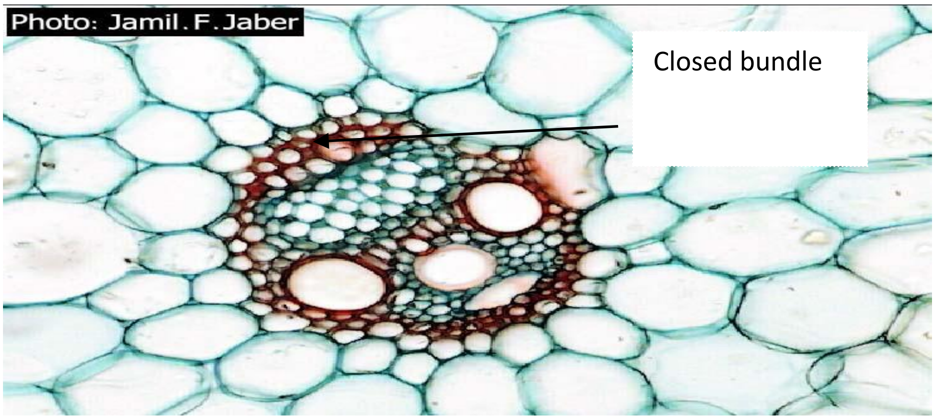
The 1st group are ***collateral bundles,*** the bicollateral bundles have phloem on the outside and inside of the xylem.

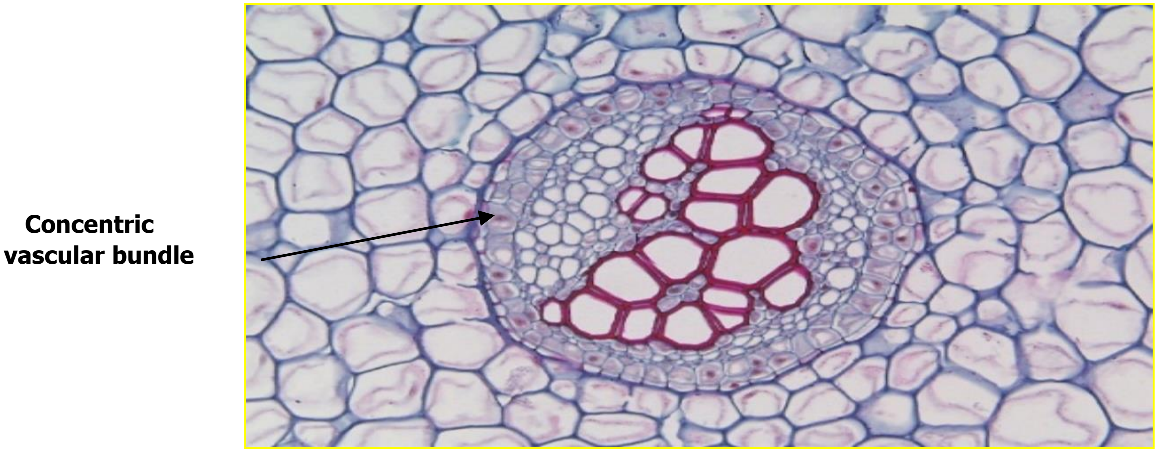
The 2nd group are known as ***concentric bundles,*** the type in which the phloem surrounds the xylem is

amphiceribral, if the xylem surrounds phloem it is ***amphivasal.***

The third is the ***radial bundles*** and is best called radial arrangement because both xylem and phloem are separated.

The terms endarch, mesarch and exarch are also used to describe the bundle in relation to the arrangement of the protoxylem.





Occurrence of Bundle Types:

Collateral bundles are common in stems and leaves of angiosperms and most gymnosperms. Bicollateral bundles occur in some angiosperms stems as for example in plants belonging to the family ***Cucurbitaceae. Amphiceribral*** bundles are common in ferns. ***Amphivasal*** bundles are rare and occur in some monocots. Radial arrangement occurs in roots.

THE PRIMARY VASCULAR SKELETION

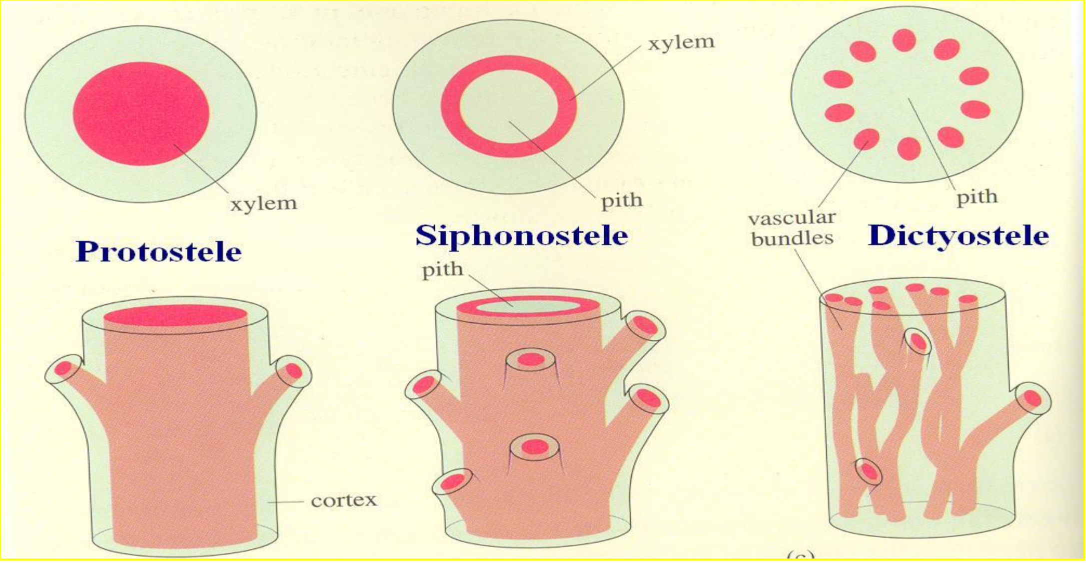
The stele:

The vascular tissues of the stele in their simplest condition form a solid rod-like column in which the phloem surrounds the xylem. This kind of stele is known as protostele. **The protostele** is a simple kind of stele and also primitive. Other types of steles are thought to have evolved from protostele.

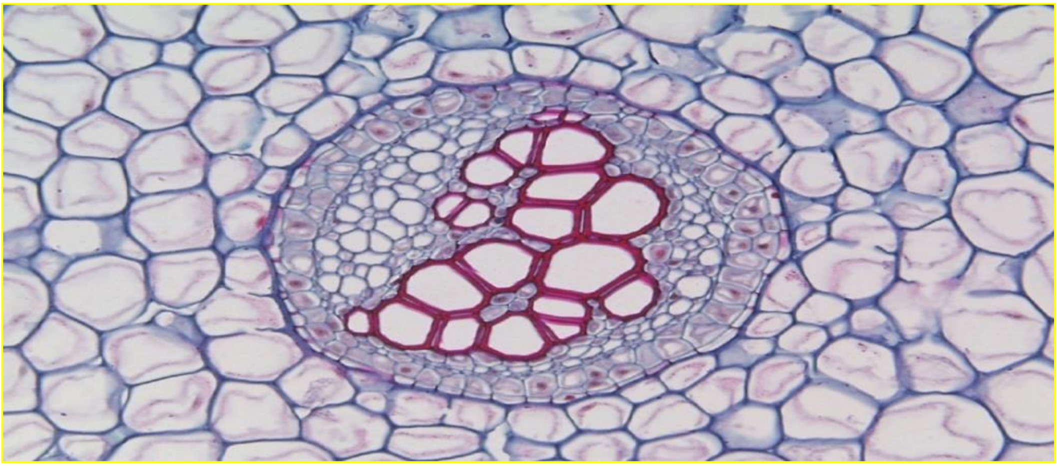
A kind of stele differing from this type in which a pith is present in the center is called ***Siphonostele*** or ***solenostele***. Two types of siphonosteles are found:

Ectophloic where phloem occurs only on the outside of the xylem and ***Amphiphloic*** where phloem occurs in both sides of the xylem.

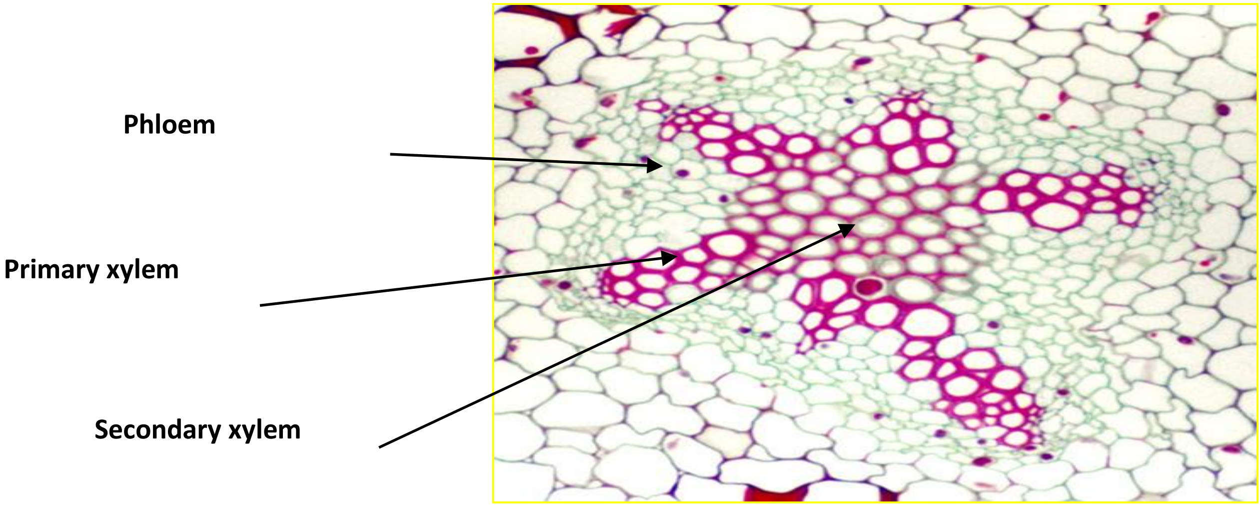
When the siphonostele is broken up into several longitudinal strands it is called ***Dissected siphonostele*** or dictyostele. In monocots the vascular bundles are



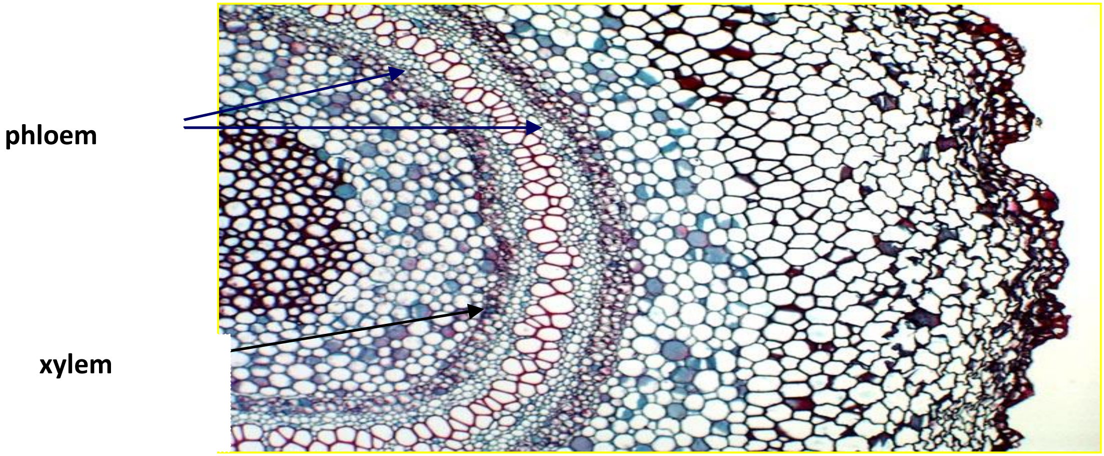
Stages of development of stele


.

Protostele

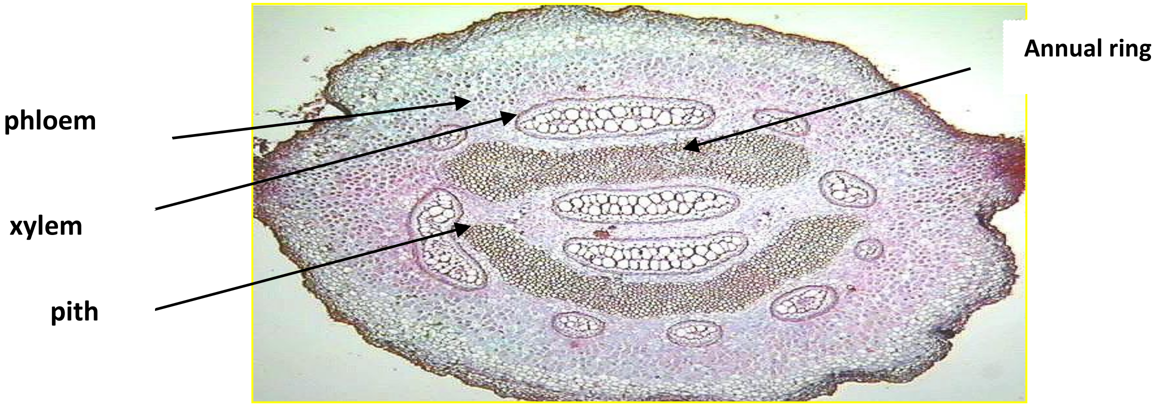


Actinostele

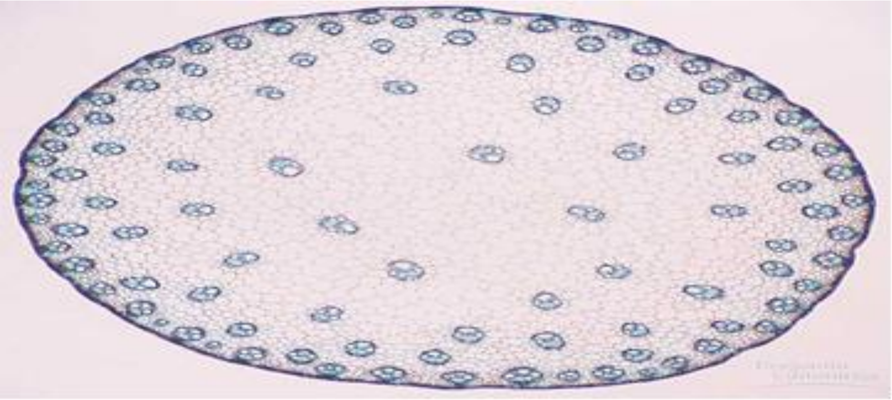


Amphiphloic siphonostele

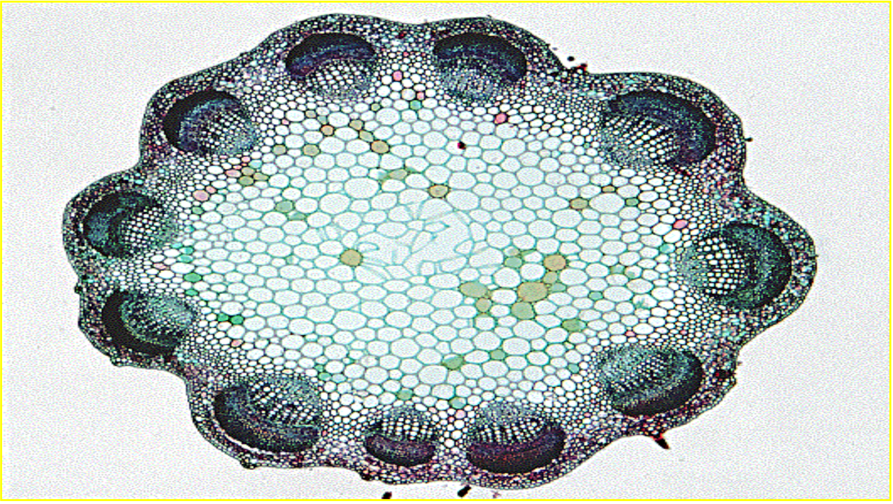
Monocyclic Dictyostele



Polycyclic Amphiphloic Dictyostele



Attactostele



Eustele

scattered and the resemblance to stele is lost. This type of stele is known as **attactostele.**

The term ***Monostele*** is used to describe the protostele since the vascular tissues form a unit structure. ***Polystele*** describes the vascular tissues which are present in strands. Therefore. protostele and siphonostele are monostele and dictyostele. In a polystele, when the dissected siphonostele is amphiphloic it is composed of protosteles and is called multiple protostele.

Two theories exist to describe the evolution of siphonostele from protostele, these are:

1- The expansion theory:

It states that the central portion of the stele does not become vascular but forms the pith. Therefore, the pith is morphologically vascular tissue.

2-The invasion theory:

It states that the cortex has invaded the central cylinder in the courses of evolution, therefore the pith is not steler in nature.

Occurrence of stelar types:

The protostele is primitive and occurs in few ferns and roots of plants.

The siphonostele is found in stems of most plants ectophloic siphonstele is characteristic of stems of gymnosperms and some angiosperms, whereas the amphiploic type is found in ferns and some families of angiosperms.

The dissected siphonostele occurs in ferns and in angiosperms.

Dissection of siphonostele is considered to result from the following:

1- Overlapping of leaf and branch gaps.

2- Dropping out of segments of the cylinder during evolutionary development

Leaf traces:

Prolongations of the stelar vascular tissues that supply the leaves are the leaf traces. The term “trace” is used to describe the bundles from the point of origin in the main axis to the base of the leaf. Structurally, leaf traces are formed of 1ry vascular tissues. The traces supplying a leaf range in number from one to many and the number is constant for a particular species and even for a family. These number is the number of bundles that leave the stele, they may fuse or branch in the cortex. In the petiole these bundles are not called traces.

Branch traces:

The primary vascular supply to lateral branches is also from the main axis. These strands are branch traces. Usually, two traces come out for each branch, which unite after short distance forming a complete stele. When single trace is formed it has the shape of a horseshoe.

Leaf and branch gaps:

Due to the formation of traces, openings are formed in the main axis stele, these are called gaps which may be leaf gaps or branch gaps. Leaf gaps occur in ferns, gymnosperms and angiosperms (pteropsida) but not in mosses, horsetails (lycopsida). Branch gaps are present in all vascular plants which possess a pith. In protostele no gaps are formed. Gaps are not associated with root traces.

In gymnosperms and angiosperms, leaf gaps are small. In ferms leaf gaps are large. Branch gaps are commonly larger than leaf gaps.

The breaking of the vascular cylinder by gaps:

The vascular cylinder is broken up in different degrees by the presence of leaf gaps. Where the gaps are small and of limited number, the cylinder is slightly brocken by them, where they are large and elongated the stele is dissected. Where the leaf gaps are numerous and overlap the stele is dissected into a number of separated bundles which is increased by branch gaps.

The number of leaf traces in plant groups:

- **Pteridophytes**: There is usually one trace.
- **Gymnosperms:** There is one or two traces.
- **Angiosperms:** There is three, five or many traces.

The number of traces may be decreased due to fusion.

The dissection of the vascular cylinder:

Additional breaking up of the vascular cylinder other than by leaf gaps and branch gaps may have been formed during evolutionary development by reduction in the amount of primary vascular tissue resulting in the formation of strips which are separated by interfascicular rays of parenchyma tissue. These are closed latter on by vascular tissues formed during secondary thickening.

THE PERICYCLE

It is a thin cylinder of tissues surrounding the vascular cylinder. It is composed mostly of few layers of cells limited internally by the 1ry phloem and externally by the endodermis. where there is no endodermis it usually mixes with the cortex. It consists of parenchyma as in most roots of angiosperms and stems of pteridophytes. The pericyclic fibers perhaps belong to the primary phloem. Study of the ontogeny of this region is necessary for determination if the pericyclic fibers are phloem fibers or not.

It is questioned whether no pericycle is present in the stems of many angiosperms because the fibers which were though to belong to the pericycle may belong to the phloem.

In roots the pericycle is parenchymatous. This layer is the region of origin of the meristems which form lateral roots and the 2ry cambium in anomalous 2ry thickening. In old roots the cells of the pericycle may become lignified or even suberized. The parenchyma cells of the pericycle function in storage also. Secretory cells and other specialized cell types may occur in the pericycle.

THE ENDODERMIS

It is formed of one layer of cells separating the stele from the cortex, it has no intercellular spaces. Endodermal cells are elongate, with the long axis parallel with axis of the stem and the end walls transverse. In cross section they are elliptical with the long axis is a tangential direction. The cell contents are like parenchyma cells.

Endodermal cells are two types: thin walled and thick walled. In the 1st type, the walls are thin and thickened with bands of lignosuberin known as ***Casparian strips*** that run completely around the cell on the radial and end walls. These pands may be thin or broad and may cover completely the radial walls. In cross section, the strips are often called casparian dots. This thin-walled type of endodermal cell is called **1ry type**.

In the thick-walled type, the radial and inner tangential walls and sometimes all the walls are thickened. This type is called **2ry type**. In this type, thin-walled cells known as passage cells which have no suberized areas are present against the protoxylem in roots. The 1ry type occur in pteridophytes and in most dicots, the 2ry type is characteristic of monocots.

Occurrence and position of endodermis:

The endodermis is sometimes considered to be the inner most layer of the cortex and the outermost layers of the stele. It is cortical in origin because in roots it is derived from the same mothers' cells of the inner most layer of the cortex. However, it has been shown that in stems it may be formed from the procambium mother cells.

In some plants an inner endodermis is present which limits the vascular tissue on the inside and separate it from the pith as in **Equisetum.**

The endodermis not only limits the vascular tissue of the axis but may also surround the vascular bundles as in **Polypodium.** In many gymnosperms, it is characteristic of the leaves and is absent from stems. In angiosperms it occurs in the stems of most herbaceous species. It is present in most aquatic plants. Woody stems and the leaves of angiosperms mostly have no endodermis.

Function of endodermis:

It appears that the endodermis functions in controlling the diffusion of water between the cortex and the stele as shown from the following:

a- It always lacks intercellular spaces and,

b- The presence of casparian strip makes the radial and end walls impervious to water, therefore, limiting the lateral diffusion between cortex and stele.

c- The presence of passage cells in case when thickening is of the secondary type.

The endodermis also serves to maintain pressure relations in the stele and prevent the accumulation of air in the conductive tissue.

It was also suggested that the endodermis may function in mechanical support and protection of the stele when the outer cortical cells are lost.

The presence of starch in the endodermis in stems may suggest that it may function in storage of food.

THE CORTEX

It is the portion of the axis that surrounds the central cylinder and is separated from it by the endodermis. It is limited on the outside by the epidermis. This definition usually is used for the 1ry cortex which is 1ry in origin. The cortex varies in thickness from a few to a great number of rows of cells. It is essentially formed of parenchyma cells, but may contain collenchyma, fibers sclereids and secretory cells. Collenchyma may be present in patches or forming a continuous cylinder under the epidermis. Fibers may be present in strands or form a continuous layer below the epidermis. The cortical parenchyma may contain chloroplasts (chlorenchyma).

The cortex of roots is more homogenous than that of the stem and usually consists of parenchyma.

The various cell types in the cortex serve various functions, but the cortex is primarily a protective layer. Other functions as support, photosynthesis and storage are secondary.

THE PITH

It is a cylindrical portion of tissue enclosed by the vascular tissue. Its surface may be furrowed and ridged due to the inward projection of the protoxylom.

The pith is made of a uniform tissue, chiefly, parenchymatous in which the cells are arranged loosely, often with obvious intercellular spaces. The cells vary greatly in shape, but they are mostly isodiametric or cylindrical with thin cellulose walls. Lignified parenchyma and sclereids may be present. Fibers occur rarely since they occur mainly in the outer tissues and the vascular cylinder. Chlorenchyma are absent although it may be present in rare cases in leafy shoots. The cells of the pith remain alive for long time and in woody plants the living cells serve as storage cells and become filled with starch and fatty substances.

Structurally the pith is like the cortex, intercellular spaces, secretory tissue, and cell contents are similar except for abundance of protective and supporting tissues in the cortex.

Developmentally, the pith cells mature very early, the surrounding tissues are meristematic and continue to elongate so that the pith may be torn to a greater extent. If there is marked increase in diameter at the same time a hollow pith is formed. This condition is common in herbs and rare in woody plants. When destruction is less extensive, cavities or canals of various shapes are formed.

The pith persists indefinitely in nearly all plants. In woody stems, the changes taking place in heart wood affects the pith, but till this stage is reached the pith remains alive. The pith is not crushed during 2ry thickening. Only in few stems in which anomalous 2ry growth is taking place as in **Aristolochia** some crushing occurs during 2ry growth. No changes occur to the pith from the primary state and the pith of old trees is like that of the young condition.

Roots generally have no pith, and when it is present, it is similar to that of the stem of the same plant, but it is more homogeneous and does not breakdown. It is more cylindrical than that of the stem because the 1ry xylem points outwards.

THE EPIDERMIS

The epidermis constitutes a layer over the entire surface of the plant body. It is continuous except for the presence of stomatal openings. Typically, it consists of a single layer of cells and in few plants, it is biseriate or multiseriate.

Epidermal cells have a large central vacuole and thin peripheral cytoplasm. Leucoplasts may be present, but chloroplast are absent except in the guard cells of stomata. Mucilage, tannins, and crystals may be present. The cells are often lobed and fitted together without any intercellular spaces. The epidermal cells may be thickened at the outer and radial walls with cutting. This cutinization of the walls is important for mechanical protection and prevention of water loss.

Origin of the epidermis:

According to the tunica-corpus theory, the epidermis is formed by anticlinal divisions of the outer layer of the tunica. Where tunica and corpus are not distinct, it is formed from the dermatogen.

Function of the epidermis:

It is primarily a covering layer which protects against rapid loss of water and mechanical injury. It may function in photosynthesis (guard cells) or secretion (nectaris).

Stomata:

The openings in the epidermis through which gaseous interchange takes place between the intercellular spaces of the subepidermal cells and atmosphere are known as the stomata. Each stoma has two guard cells which have special shape together with other cells known as accessory cells.

Structure and action of the guard cells:

The guard cells of the dicots are commonly kidney shaped. The cell walls are unevenly thickened. This character plays a role in the opening and closing of the stomatal pore. They are covered with a cuticle which extends over the surfaces facing the stomatal pore and substomatal chamber in addition to the outside wall. The thinner walls of the cells are more affected by changes in turgor of the cells which is associated with the state of carbohydrates in these cells.

In some monocots as these of the Gramineae and Cyperaceae the guard cells have different shapes. From surface view they are narrow in the middle and enlarged at both ends. The center narrow part has a very thick wall, the bulbous ends have thinner walls. Opening and closing of the stoma depends on the changes in the size of the enlarged portions. The guard cells have subsidiary cells one on each side of each guard cell. The stomata of the gymnosperms are commonly deeply sunken. The characteristic features of these stomata are the walls of the guard cells and subsidiary cells are partially lignified. The presence of thin wall parts and rigid wall parts helps in opening and closing the stomata.

Development of the stoma:

In the development of the stoma in angiosperms, the mother cell of the guard cells originates by unequal division of a protodermal cell. Small cell is the mother cell, it characteristic shape of the guard cells. The intercellular substance between the guard cells swells and the connection between the two cells is weakened. They separate in their median parts and the stomatal opening is formed.

Hairs or Trichomes:

Hairs or trichomes arise from one (unicellular) or more (multi-or pluri-cellular) epidermal cells and are of varied character. The simplest are the papillae, frequently found on the petals of flowers, giving the velvety appearance of these organs. Papillae are in somewhat cone-shaped outward extensions of the exposed walls of epidermal cells. At short distance behind the growing-points of roots we find much long extensions of the outer wall of the epidermis. The wall remaining thin and the cell living and vacuolated, with a nucleus embedded in the thin peripheral cytoplasm near the tip of the hair. These are the root-hairs on account of which the name piliferous layer is given to the epidermis of the root. They enormously increase its absorbing surface.

Other much elongated, unicellular hairs, but with thick cellulosic cell walls covered with a thin cuticle, are those of the epidermis of the seed of the cotton plant (**Gossypium** species) which provide the cotton of commerce. These hairs, when fully mature, are dead and filled with air, hence their white appearance. They are also twisted and flattened. Short, thick-walled, and sharply pointed unicellular hairs, bent or curved all in one direction, make the surface of the organ which bears them rough to the touch, whilst longer, straight, stiff hairs are usually termed bristles, and may have their walls impregnated with silica or calcium carbonate. When the surface of a hair, as seen under a microscope, is raised in numerous slights, rounded projections, it is said to be warty.

When a multi-cellular hair consists of a row of two or more cells, it is described as uniseriate. Multicellular hairs may have a massive base involving several epidermal cells, but tapering to a single cell at the tip, they may be stellate, consisting of several unicellular hairs arising from a common basal cell; scale-hairs, consisting of a plate of cells radiating from a common center of attachment; consisting of a plate of cells attached laterally, capitate hairs, with a definite pedicel and a rounded or flattened head. Often such hairs are glandular. Hair other than glandular are usually classified as covering or protective. Such hairs may protect leaves and stems against excessive loss of water by transpiration. They sometimes form a felt-like layer over the surfaces of young leaves, especially in winter-buds.

Protection in another sense is afforded by such hairs as those of the (***Urtica dioica***), which consist of an elongated, tapering hair whose broader, rounded base is embedded in a columnar mass of epidermal cells. When a hair is touched, the brittle siliceous point of a hair breaks and a puncture is made in the skin. The contents of the hair, which were evidently under pressure, are forced into the skin by the release of the pressure, assisted by a contraction of the base of the hair. The hair contains at least three active substances of which histamine and acetylcholine appear to be responsible for the irritating, burning sensation.

Emergencies:

Stronger outgrowths are often found on the surface of the plant. They differ from trichomes in containing a core of cortex (occasionally also vascular tissue) and not being outgrowths of the epidermis alone. Such outgrowths are called emergencies. Frequently they are of the nature of prickles, as, e.g., in the rose. Other examples are found in the membranous outgrowths, called ligules, of many leaves, e.g., the leaves of grasses.

SECONDARY GROWTH IN STEMS

Secondary growth increases the number of Vascular tissues in stems beginning with the part of the shoot axis that has ceased to elongate. It contributes only to the thickness of the axis. The secondary growth is characteristic of the gymnosperms and of woody dicots and is found in variable amount in the herbaceous dicots. Some herbaceous dicots and most monocots have no 2ry thickening. The 2ry growth in monocots is of special type.

The 2ry growth includes the formation of 2ry vascular tissues and of periderm:

The vascular cambium:

The vascular cambium arises in part from the procambium within the vascular bundles and it part from the interfascicular parenchyma. The parts of the vascular cambium arising in these two positions are called interfascicular and interfascicular cambium. In plants in which secondary growth takes place a part of the procambial cells remains meristematic and give rise to the interfascicular cambium. Since the maturation of procambial cells usually proceed towards the center of the procambial strand, the cells in the central region are the last to mature. These last central cells are not transformed into xylem or phloem cells, but remain meristematic, these are the interfascicular cambium. The meristematic strips developing across the rays and connecting the vascular cambium within the bundles is the interfascicular cambium.

In the most common type of secondary growth, the vascular cambium becomes a complete cylinder and produces continuous cylinders of secondary vascular tissues.

Secondary vascular tissues:

The new cells produced by the division of cambial cells mature as secondary xylem elements and as secondary phloem elements. Secondary xylem is laid down on the outer side of the primary xylem and the secondary phloem on the inner side of the primary phloem. Of the two cells resulting from the division of a cambial cell, only one matures and the other remains meristematic.

The vessel element or tracheids of secondary xylem are of the pitted type. Occasional wood fibers and wood parenchyma cells are also produced. Sieve tube elements or sieve cells of the secondary phloem do not differ significantly from these of the primary phloem and are associated with phloem fibers and phloem parenchyma. Secondary xylem elements are heavily lignified. They are hard and comparatively incompressible, in contrast to the thin-walled and delicate phloem cells.

Secondary rays, called vascular rays, which supplement the pith rays are also formed by the cambium. These may be initiated at various points in the secondary xylem and extend outwards to or through the phloem. They have limited vertical extant and are like small sheets of parenchyma inserted among the vascular elements. Like the pith rays, they are pathways of lateral movement of materials. The cells may contain starch and crystals.

Effect of cambial activity upon the primary plant body:

Formation of 2ry vascular tissues creates considerable stress in the interior of the stem. The 1ry xylem becomes separated from the 1ry phloem by 2ry vascular tissue. The 1ry xylem and pith remain in their position covered with 2ry xylem and their parenchyma may remain alive for many years. Sometimes the pith is crushed and the conducting elements of the 1ry xylem become nonfunctioning because of 2ry thickening.

The 1ry phloem is pushed outwards and, in most cases, it becomes nonconducting. The cortex may persist for many years. It may increase in circumference by the enlargement of their cells and through divisions. The epidermis may persist by growing through cell enlargement and divisions.

With continued accumulation of 2ry tissues the 2ry phloem also is subjected to pressure from the inside because of the enlarging 2ry xylem. The phloem may resist pressure and increase in circumference, and due to the presence of phloem fibers and remain functioning. In other species without fibers old phloem may be completely crushed. The increase in circumference of the phloem is the result of increase in cell size of phloem parenchyma and parenchyma rays and also by their divisions. The rays therefore appear wider than usual.

Effect of secondary growth on leaf gaps and traces:

The cambium arising in the leaf gaps functions as inter- fascicular cambium producing xylem and phloem. If the gap is wide, it may take a year or two for the cambium to completely develop in the gap since the cambium is being first formed along the margins and extend to the center of the gap. Therefore, the gap appears narrower and narrower due to the formation of 2ry vascular tissue and when the process to complete the gap is closed.

The leaf trace opposite to the gap undergoes complex changes. In deciduous species, the leaf trace breaks off from the leaf bundle. With increase in thickness, the bases of the leaf traces are buried. Continued secondary growth may finally result in breakage of the trace into two parts. Rupture of the leaf trace therefore results from the lateral pressure exerted by secondary growth on the trace.

The time of rupture of the trace depends upon number of factors which are:

1- The rate of 2ry growth.

2- The size of the trace.

3- The angle at which the trace leaves on the main stull.

When the trace is at right angle, to the main axis it takes longer time to break, but when the trace passes up vertically through the cortex it breaks quickly due to the lateral pressure caused by 2ry growth on the trace. The small traces break quickly than the large traces.

In evergreen leaves the traces are extended by a type of 2ry growth that increases them in length by addition of new tissues. The 1ry xylem of the trace is ruptured gradually in one oblique direction and new cells replace the destroyed cells. If the leaf persists, the upper old xylem of the trace is broken, and new cells are added from below. The gaps are not completely closed, and only close after the trace is broken which occur when leaves die.

Branch traces are buried in the same way as leaf traces but are not ruptured.

Relation of secondary growth to leaf and branch gaps:

Leaf gaps are closed by the gradual lateral extension of the cambium. The new meristematic cells arise apparently out of the parenchyma cells of the gap. The size and shape of the gap determine in part the length of time before the gap is closed. Wide gaps being closed more slowly than long narrow gaps. In most angiosperms, leaf gaps are closed in the first season. Branch gaps which are often wide and large, are closed more slowly than leaf gaps. Some branch gaps remain open until the second or seven fourth year.

Burial of branch bases:

As successive layers of xylem are laid down by the cambium, all tissues within the cambium cylinder are buried more and more deeply. In this way the bases of branches become embedded in the wood of the tree trunk. In a living branch the buried portion has the shape of an **inverted**

cone because, as new layers of the xylem are laid down over the branch, the cambium is moved by the increased in the diameter of the trunk farther and fro their away from the point of insertion of the branch in the trunk. The buried portion of the branch cannot increase in diameters because the inner portions are progressively of less diameter as the attachment to the primary cylinder is approached. When a branch dies no further increase in diameter occurs and its base in buried as a cone of dead tissues. Knots found in wood are sections of embedded branch bases, loosely or tightly held in the wood, depending on whether the branch was dead or living at the time it was formed.

Healing of Wounds:

When a stem or other part of the plant is injured the wound soon heals. Immediately after the wounding, the uninjured cells about the wound are stimulated to form a secondary cork cambium, which produces a layer of cork so that the wounded surface is soon isolated by an impermeable layer from the inner living tissues. This type of healing is readily seen in potato-tuber that has been damaged. Both Monocotyledons and Dicotyledons possess this capacity of healing.

In woody plants, if a branch is cut across, the uninjured living cells (generally the cambium) adjacent to the wounded surface produce a mass of undifferentiated parenchymatous tissue called a callus, and this may later develop on or near its surface a layer of cork. If the cambium is injured, the two cambial surfaces both produce callus tissues so that any gap between then is bridged. In this bridge of callus, a new cambium arises. The continuity of the cambium is thus achieved, and provision is made for the continued formation of secondary tissue. This is the basis of grafting in which the cut surfaces of two shoots (the stock and scion) are brought into contact and protected against desiccation so that they each form callus and units. For such a union to take place it is unnecessary for the two shoots to be of the same species, but they must be of closely related species. The shoots of two very unrelated species are rarely able to form a union. The matching of the cambia when the stock and scion are put together facilitates the establishment of cambial connection.

Heartwood is more durable than sapwood, because the reduction of food materials available for fungi and bacteria by the absence of protoplasm and starch, the formation of resins, tannins and oils and the blocking of the vessel cavities by tyloses and gums make the wood less pervious to water and less subject to attack by the organisms of decay. The presence of coloring materials also makes it more desirable. For these reasons’ heartwood is commonly of more value than is sapwood.

SECONDARY PHLOEM

Secondary phloem is an important tissue in dicots and gymnosperms since in these plants it replaces the primary phloem which becomes crushed and functionless. In herbaceous plants of limited secondary thickening and in monocots that have secondary thickening, the primary phloem remains intact. Generally, in plants with secondary thickening, the secondary phloem is the most important tissue functionally. The development of this tissue from the cambium makes possible the constant renewal of this tissue since it is of short duration.

Secondary phloem is made up of several cell types which are like those of the primary phloem. The secondary phloem, in comparison with the primary phloem, has a more arrangement of cells in radial rows, higher proportion of sieve tubes which are larger with thicker walls, shorter sieve tubes and fibers and a longer functioning life.

The proportion and arrangement of sieve cells and sieve tubes in secondary phloem varies greatly. In gymnosperms, the sieve cells make up the greater part of the phloem, parenchyma and sclerenchyma occur in small amounts. In most herbaceous plants the proportion of sieve tubes is small.

The arrangement of sieve tubes in the secondary phloem with respect to other cells vary in different plants. In **Telia** they occur in tangential rows or bands, in **Carya** they are found in groups surrounded by fibers. In most woody plants any arrangement of sieve tubes or sieve cells, parenchyma and fibers may occur. Companion cells are absent in gymnosperms but present in angiosperms. Parenchyma are found in the secondary phloem of all plants except monocots. In gymnosperms parenchyma are relatively few, whereas in young woody dicot plants (seedling) they are abundant. Fibers are characteristic of the secondary phloem. Frequently, they occur in definite tangential rows as in **Liriodendron** and **Populus**. When fibers are abundant, they provide mechanical support. Phloem fibers are common in **Vitis** stem. In gymnosperms, fibers may be completely lacking from phloem of some species or they may be abundant in other species.

Phloem rays are usually present and are variable in width and height. They may be one cell wide as in **Salix** or two or three cells wide as in **Malus** or many cells as in **Liriodendron.** Dilated phloem rays are found in **Tilia**.

Secretory canals are often abundant in the secondary phloem and the secretions may be of economic value such as rubber obtained from the latex of **Hevea**.

TYPES OF STEMS

Stems differ in their primary and secondary structure so that it is suitable to divide them into conifer stems herbaceous stems, woody stems, stems of vines, monocot stems and stems with anomalous secondary growth.

Conifer stems:

The stem of **Pinus** is used as an example of complex stems. In the primary state the stem has separate vascular bundles. The vascular cambium composed of intra-fascicular and interfascicular parts which divide to give secondary xylem and secondary phloem. The primary xylem is found next to the pith but the 1ry phloem is completely crushed. The primary phloem forms no fibers and therefore it is difficult to separate it from the cortex. The cortex contains resin ducts. The initial periderm arises beneath the epidermis and is not replaced by deeper periderms for many years.

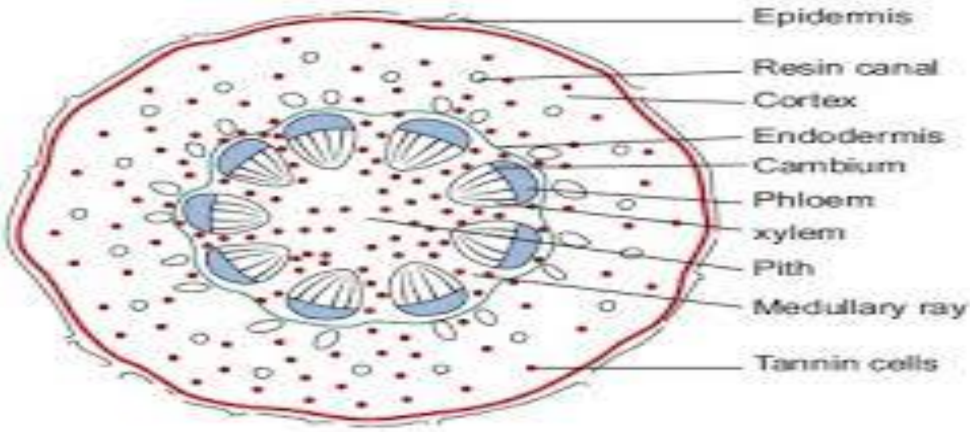
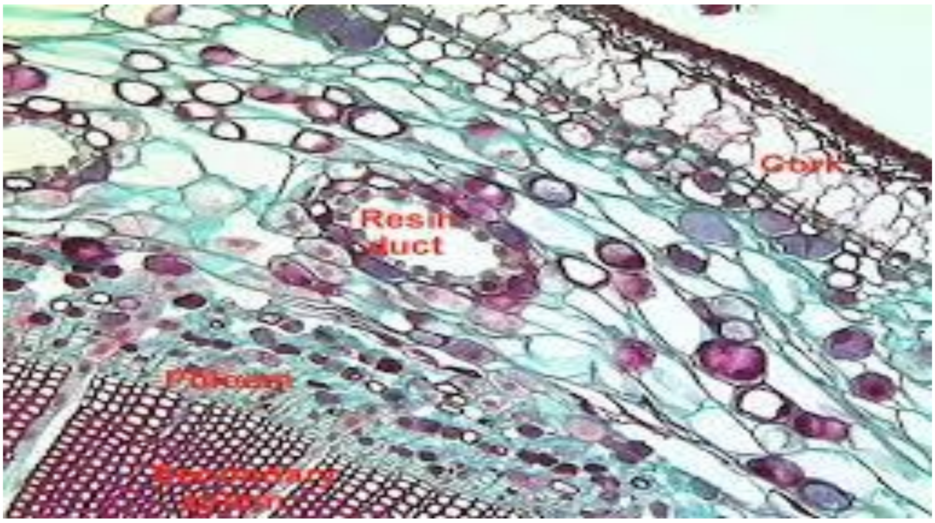
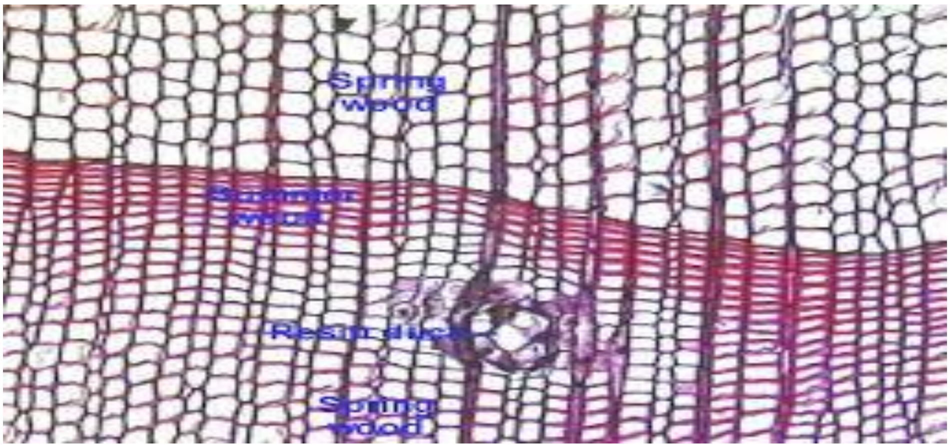


Figure 2.50: T.S. of *Pinus* stem



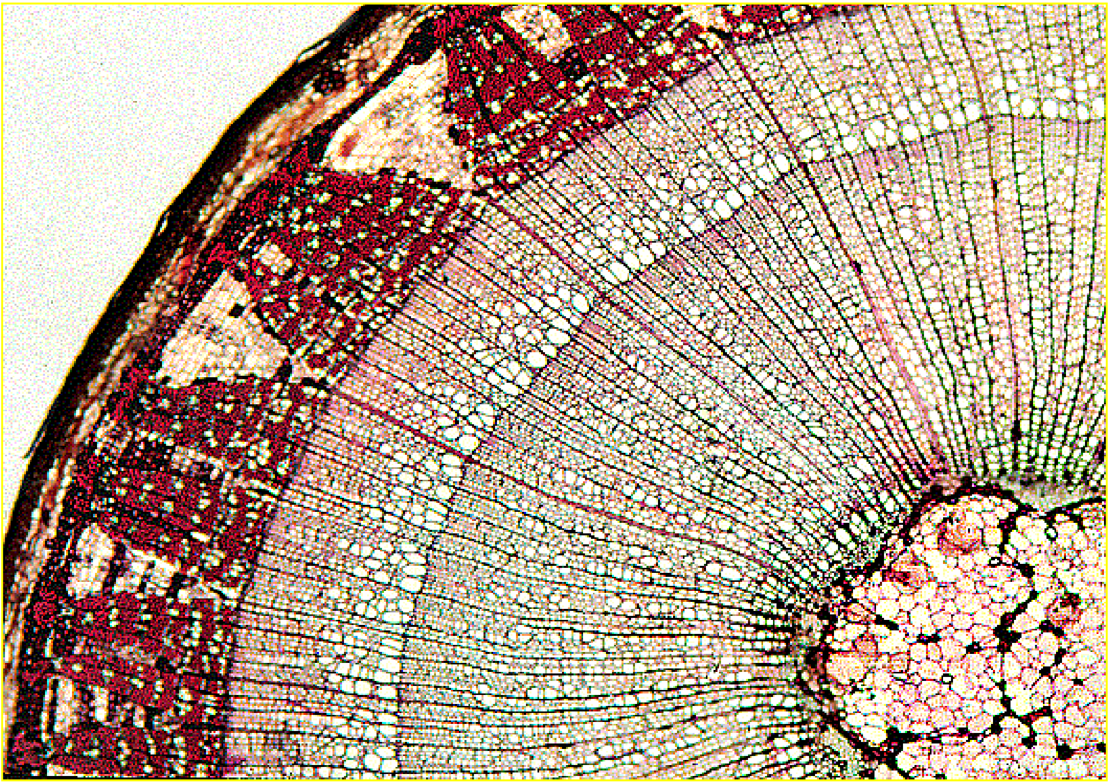


Woody dicot stems:

Variations occur in the stems of dicots in the distributions of vascular bundles and interfascicular regions. In most dicots, the interfascicular regions are narrow or very narrow as in **Tilia, Salix**, **Quercus,** and **Prunus.** In all these species the 2ry tissues form a continuous cylinder.

Tilia illustrate some of the common features of the woody dicot stems. On the inner edge of the continuous secondary xylem, the primary xylem has slightly uneven outline around the pith. The secondary xylem has a denser appearance than the primary and contains vessels, tracheids, fibers and xylem parenchyma wide and narrow rays are present. The 2ry phloem has characteristic appearance because of dilatation of rays and the alteration of bands containing fibers and bands containing sieve tubes, companion cells, and parenchyma.

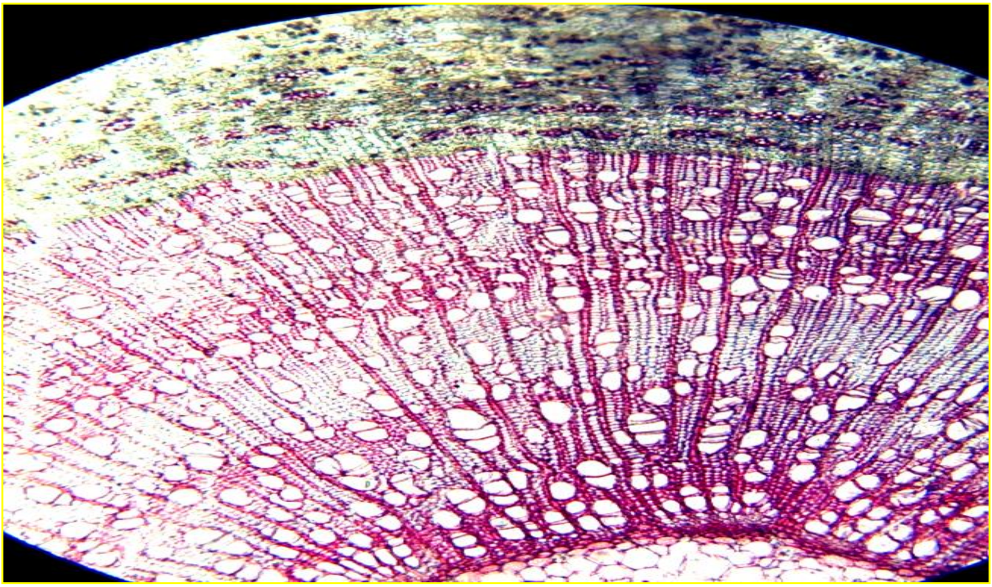
The initial periderm arises beneath the epidermis and persists for many years. The cortex is retained during this time. The cortex is early differentiated from the primary phloem because the latter contains fibers in its peripheral part, as well as in the deeper parts. The pith is parenchymatous. The outer part of the pith may remain active for storage.



T.S.in woody stem plants (*Telia*)

1. Presence of periderm.

2. Secondary phloem contains fibers.
3. Large amounts of 2ry xylem differentiated into spring and autumn wood forming annual rings.



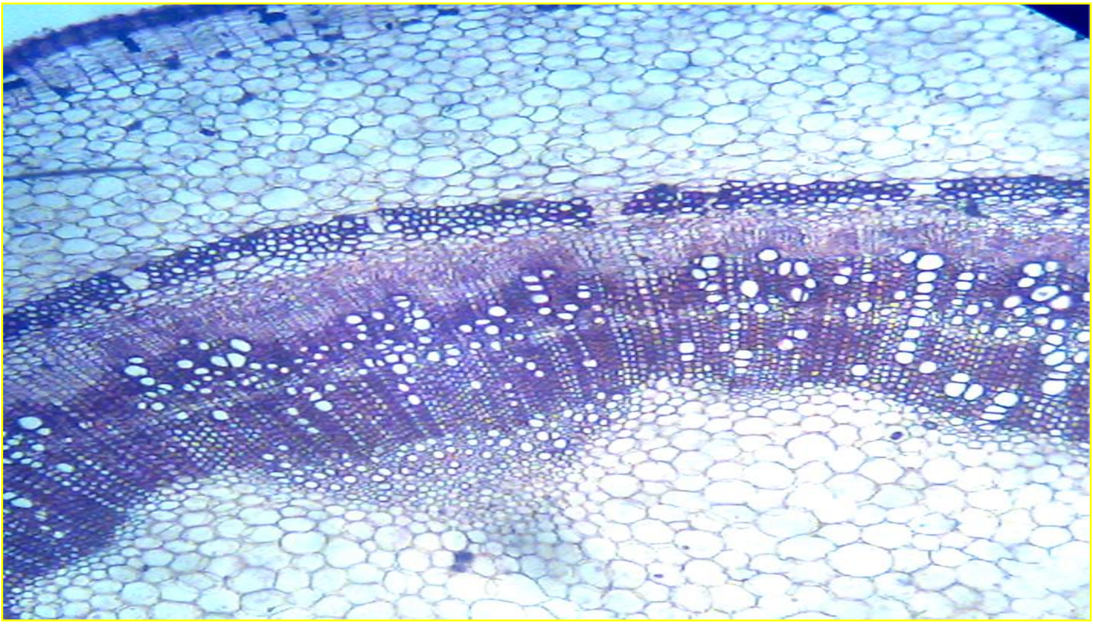
- **Section in Old Dicot Woody Stem** (***Salix***)
- The supporting tissue under the epidermis is collenchyma.
- The secondary tissues form a continuous cylinder and the interfascicular regions are very narrow.
- Large amounts of 2ry xylem and secondary phloem.

Herbaceous stems:

Herbaceous stems have no distinctive anatomical structure. Many herbaceous dicots have secondary growth of the ordinary type and therefore resemble young woody dicots. Stems of **Helianthus** and **Ricinus** have distinct interfascicular regions in which the interfascicular parts of the cambium arise. The 1ry phloem has fibers and therefore can be easily separated from the cortex. The vascular cambium forms continuous cylinder.

In **Pelargonium**, the vascular bundles are very close to each other so that the interfascicular regions are difficult to distinguish. The secondary tissue forms a complete cylinder. The vascular region is surrounded by several rows of primary phloem fibers. In old stems the epidermis is replaced by periderm.

In the stems of **Medicago** and **Trifolium** the vascular bundles are clearly separated from one another by wide interfascicular regions. The interfascicular cambium produces cells mostly on the xylem side and these are sclerenchyma cells.



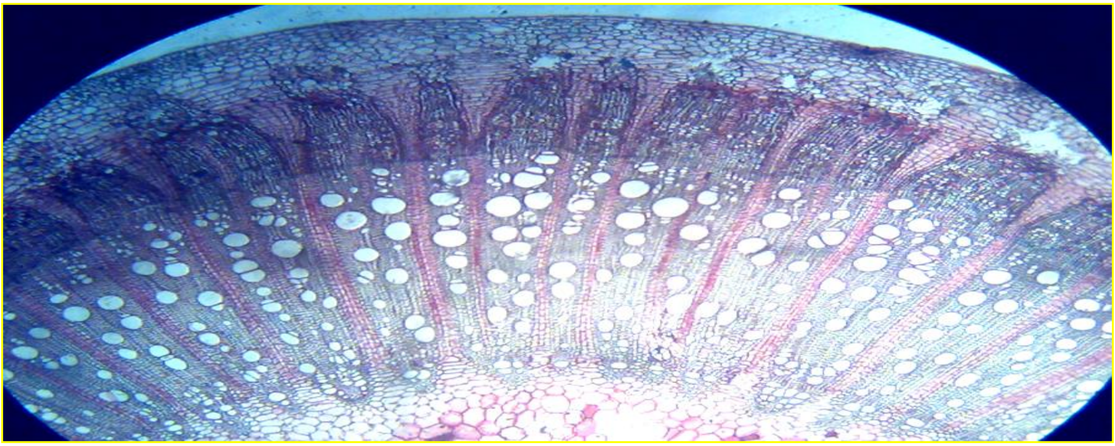
- Section in ***Pelargonium*** Old dicot herbaceous stem

Stems of **Ranunculus** have no 2ry growth. In species with internal phloem such as members of solanaceae, (as tomato, potato, tobacco) 2ry growth occurs in these stems, the cambium appears only between the outer phloem and the xylem.

Dicotyledonous vine stems:

The common characteristic of vine type of stems is the presence of very wide rays so that the secondary vascular tissue appears to consist of strands. The stem of **Vitis** is a good example for the vine type stems. In the primary state, the vascular system consists of strands of various sizes, the interfascicular cambium is formed and a continuous vascular cambium cylinder is formed. The interfascicular cambium forms parenchyma so that the wide rays are formed. The primary phloem has fibers which makes primary phloem clear from the cortex. The secondary phloem also contains fibers. The innermost layer of the cortex is the starch sheath, the pith is composed of parenchyma cells.

The periderm arises not beneath the epidermis but deeper, it first appears in the primary phloem, then it appears latter from 2ry phloem. The separation of the vascular tissues into strands is clearer in **Aristolochia** stem.



- Section in ***Vitis*** Old dicot vine stem
- Primary and secondary xylem are on the same radius.
- Medullary rays are numerous and narrow (2ry vascular tissues appear to consist of strand.
- Secondary xylem and phloem are large.

Cucurbita stem is also similar but has much less secondary growth. The bicollateral vascular bundles appear in two series, an outer and an inner. They are embedded in ground parenchyma. The inner part of the pith breaks down in early states of primary growth. The vascular bundles are enclosed by a cylinder of fibers. The cortex is composed of parenchyma and collenchyma and ends to the inside with starch sheath. Secondary growth is limited to the vascular bundles.

■ Section in ***Luffa*** Old herbaceous dicot stem

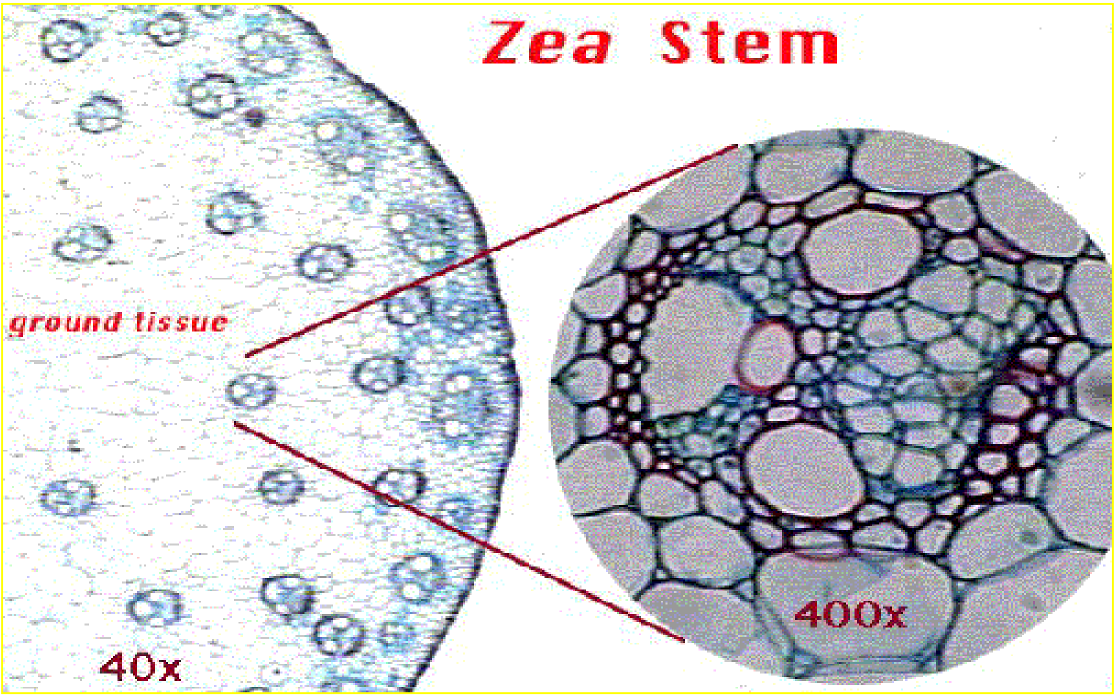
1. The supporting tissue under the epidermis is collenchyma (angular).
2. The V.B. are arranged in two rows.
3. Bundles are bicollateral.
4. No cambium between the xylem and inner pohloem

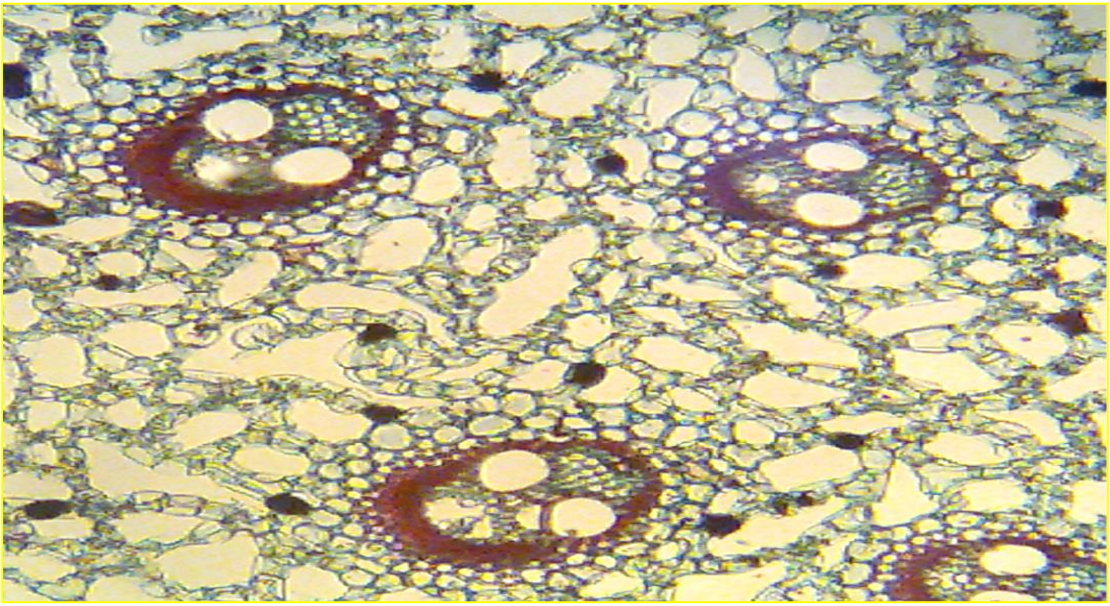
Monocot Stems:

Grass stem: The Gramineae have widely spaced vascular bundles not arranged in one circle in transverse section. The bundles either are in two circles such as in **Avena**, **Hordeum**, **Secale,** **Triticum** and **Oryza** or are scattered throughout the section such as in **Bambusa**, **Saccharum**, **Sorghum** and **Zea**. In grasses with circular arrangement of bundles a continuous cylinder of sclerenchyma occurs close to the periphery. The outer smaller bundles are embedded in this sclerenchyma. Fiber strands occur between these bundles and the epidermis, and strands of chlorenchyma alternate with the fiber strands. Stomata occur in the epidermis adjoining this chlorenchyma. The pith often breaks down except-near and at the nodes in grass stems that have the bundles arranged in circles. In stems with scattered bundle no cylinder of sclerenchyma develops, but the subepidermal parenchyma may be sclerified. In both kinds of stems the vascular bundles are entirely primary and are enclosed in sheath of sclerenchyma.

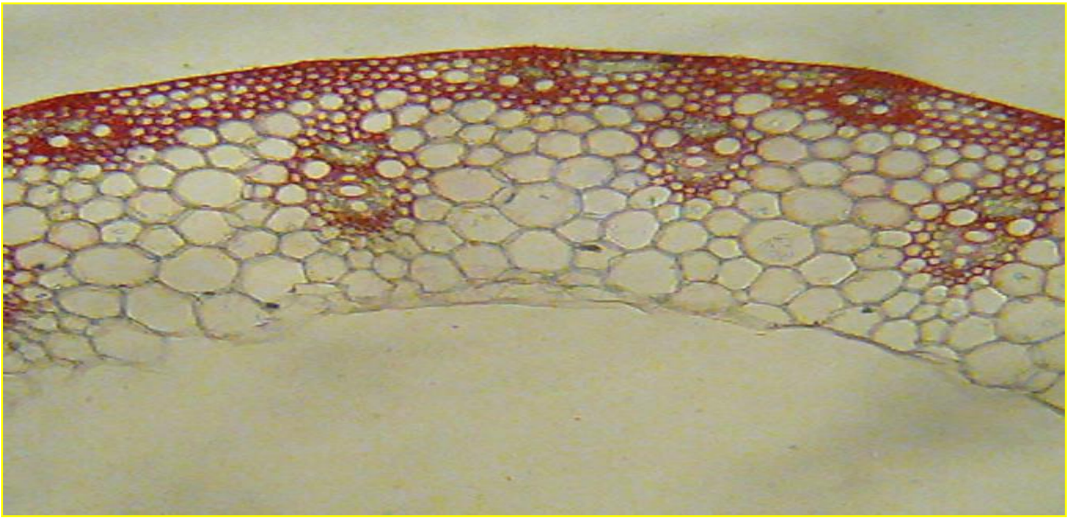
Monocot stem is characterized by:

1. The supporting tissues under the epidermis is fibers.
2. Vascular bundles are scattered.
3. Ground tissue undifferentiated into cortex and pith.
4. Xylem vessels arranged in V- or Y- shape.
5. Vascular bundles are closed collateral.
6. The phloem is regular.

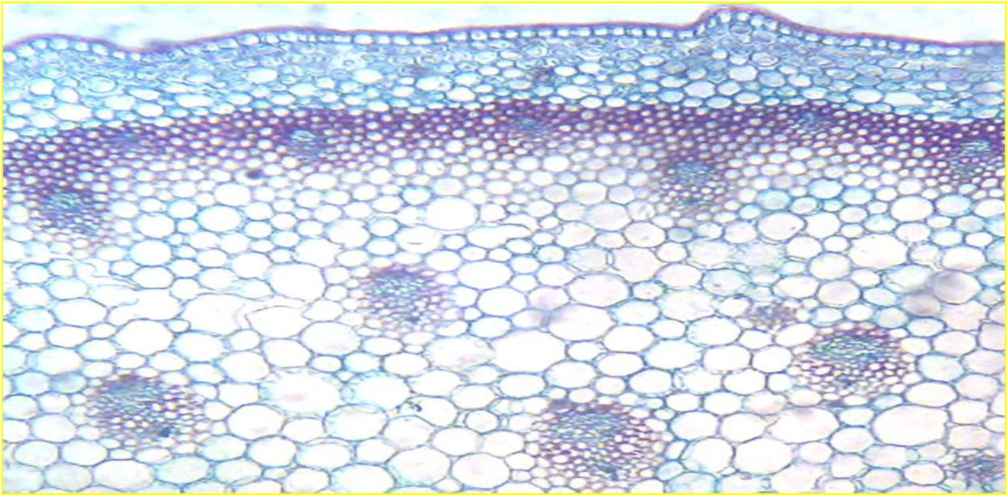




- **Section of *Cyperus* stem**
- Section shape is triangular
- Scattered vascular bundles
- Hypodermal fibers are in batches.
- Outer layer of ground tissue is parenchyma and the inner is aerenchyma

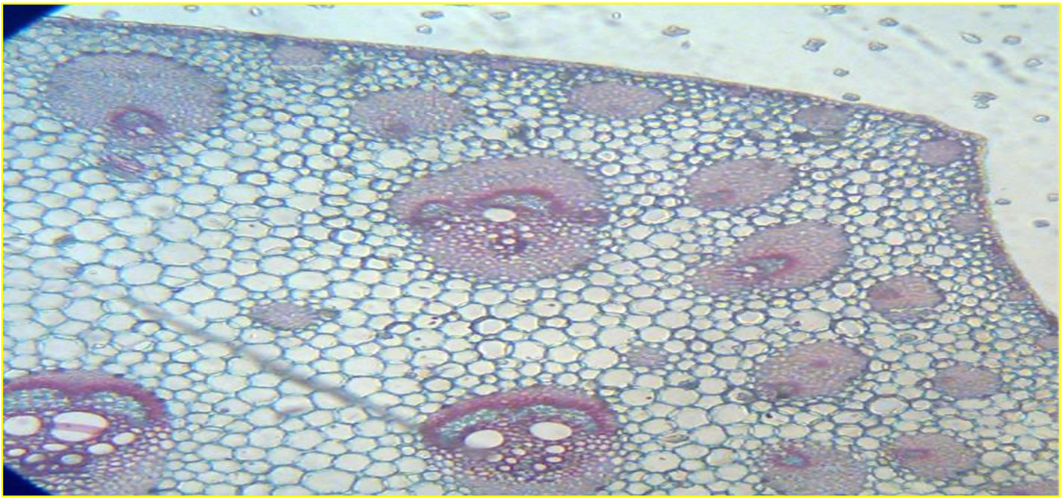


- Section in ***Triticum*** stem
- Hypodermis is a continuous layer of Fibers
- vascular bundles are arranger in two rows
- The outer smaller bundles are embedded in the hypodermal fibers
- Xylem shape is V-shape
- The stem is hollow

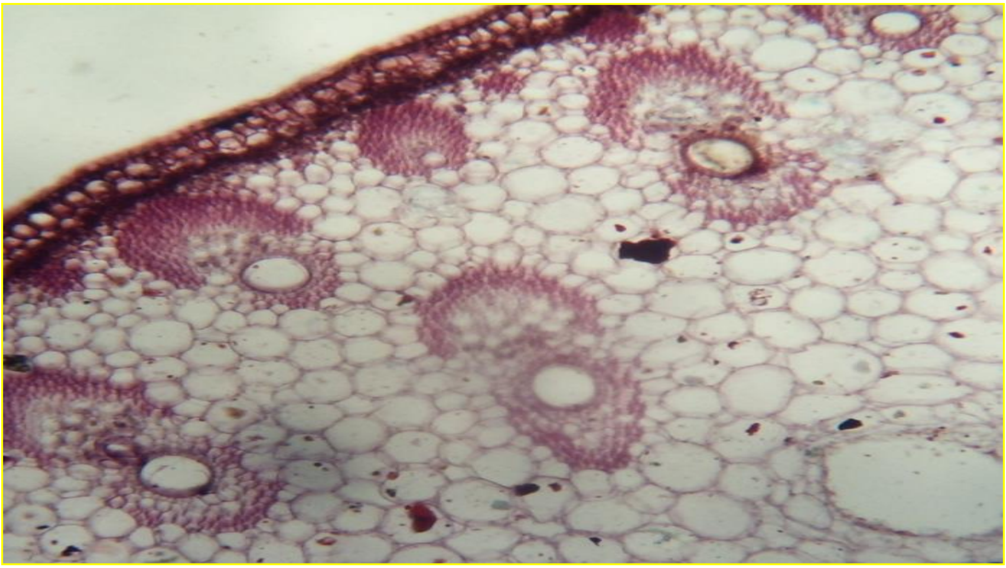


- Section in ***Ruscus*** stem
- vascular bundles are scattered

- The cap fibers is present on each vascular bundle



- Section in ***Phoenix*** stem
- The hypodermal fibers are formed in batches
- Thick bundle sheath.
- Xylem form U-shaped



- Section in ***Canna*** stem
- The epidermis is followed by chlorenchyma layer
- Hypodermal fibers are in batches.
- The xylem shape is made of one vessel only.

Monocotyledons usually lack secondary growth but may develop thick stem as in plans by primary growth alone. Secondary growth occurs in herbaceous and woody Liliflorae as **Aloe, Dracaena** and **Yucca** and is referred to as anomalous growth and will be mentioned latter.

Anomalous Secondary Growth in Stems:

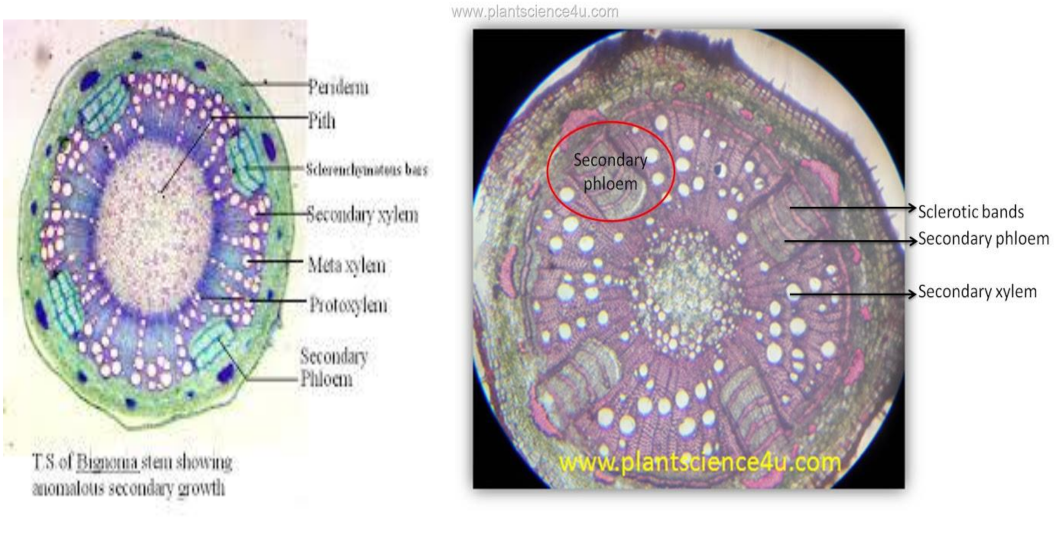
a) Dicot stems:

There are two types of anomalous secondary growth in dicot stems:

1- Those in which the cambium develops in its normal position, but the secondary tissues show unusual and irregular distribution.

2- Those in which both the cambium and the secondary tissues are abnormally arranged.

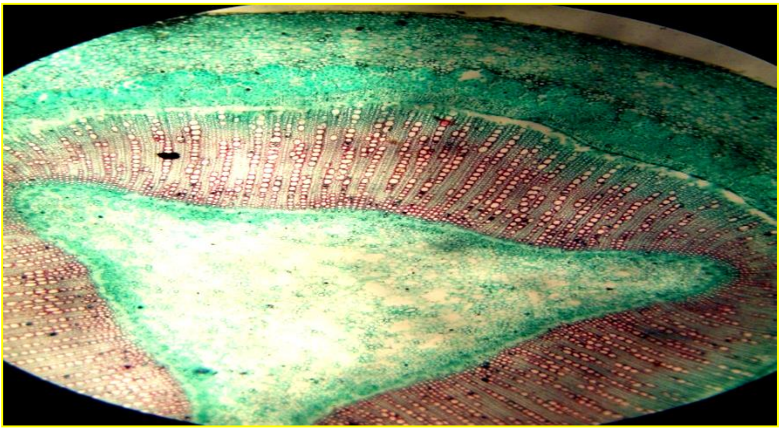
In the first case for example, the cambium is normal in its position and is found between xylem and phloem, however it is irregular in its activity and develops vascular tissues of unusual arrangement and proportion of xylem and phloem. Example of this case is found in **Bignonia** sp. in which the cambium forms in some segments much larger proportions of xylem than of phloem and in others more phloem than xylem.



Bignonia sp.

This type of activity results in a ridged and furrowed xylem cylinder. Restriction of activity of the cambium to certain regions also results in the formation of flattened stems as in **Jacaranda**.

- ***Jacaranda*** stem:
- The cambium is normal in its position (between xylem and phloem).
- The cambium is abnormal in its activity (form equal amounts of secondary phloem but unequal amounts of xylem).

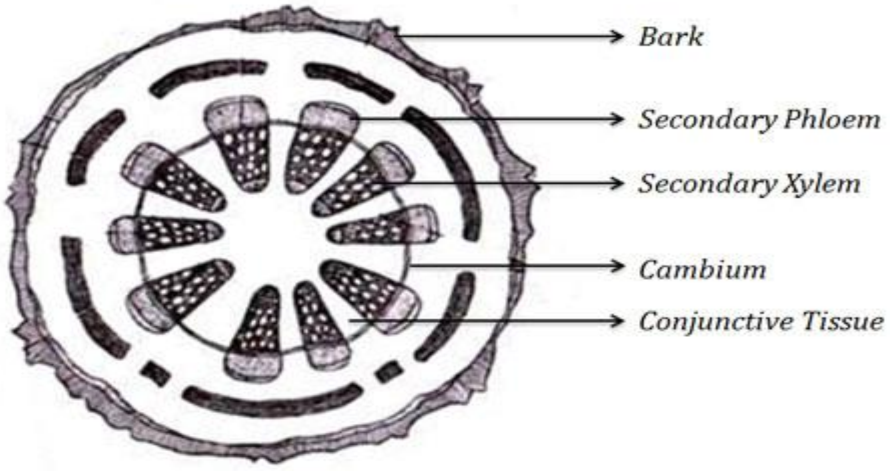


Abnormal Old Dicot Stems

- ***Nerium*** stem:

- The cambium is normal in its position (between xylem and phloem).
- The cambium is abnormal in its activity (form equal amounts of secondary phloem but unequal amounts of xylem).

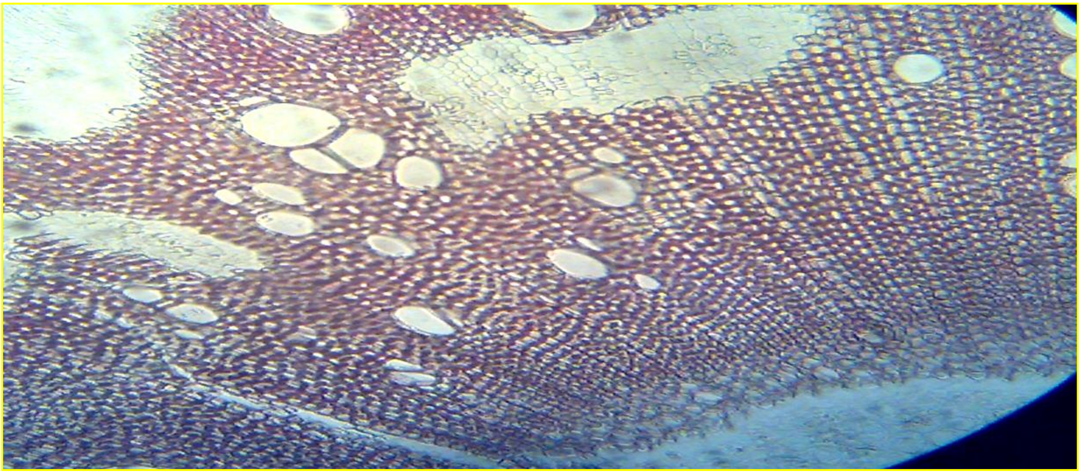
In **Aristolochia** segments of cambium form only ray like parenchyma and with increase in diameter new areas of cambium are constantly given over to the formation of rays of parenchyma. The vascular cylinder is therefore highly segmented.



Anomalous Secondary Thickening in Aristolochi

In the second case in which the cambium and the secondary xylem and phloem are abnormally arranged is exemplified by **Amaranthus** and **Chenopodium**. In these cases, there is first formed irregularly arranged bundles which are partly of secondary nature. In these bundles' normal cambium functions only for short period giving secondary vascular tissues limited to the bundles only. Its activity soon ceases, and a new secondary cambium arises in the pericycle just outside the bundles. The cambium forms separate secondary bundles composed of xylem and phloem embedded in nonvascular tissue. This embedding tissue is also called conjunctive tissue or intermediate tissue which consists of elongate lignified cells. Bundles are formed to the inside whereas to the outside very little parenchyma or no cells at all. The bundles may be irregularly arranged or in definite concentric rings.

In another type of activity, the cambium produces interxylary phloem. This case is found in ***Leptadinia***, in which secondary phloem tissues are found embedded in the secondary xylem. This occurs due to the division of the cambium cells at some position in the cambium cylinder to give phloem to the inside and outside for short period, then divides again normally to give phloem to the outside and xylem to the inside, the refer parts of the phloem are buried in the secondary xylem.

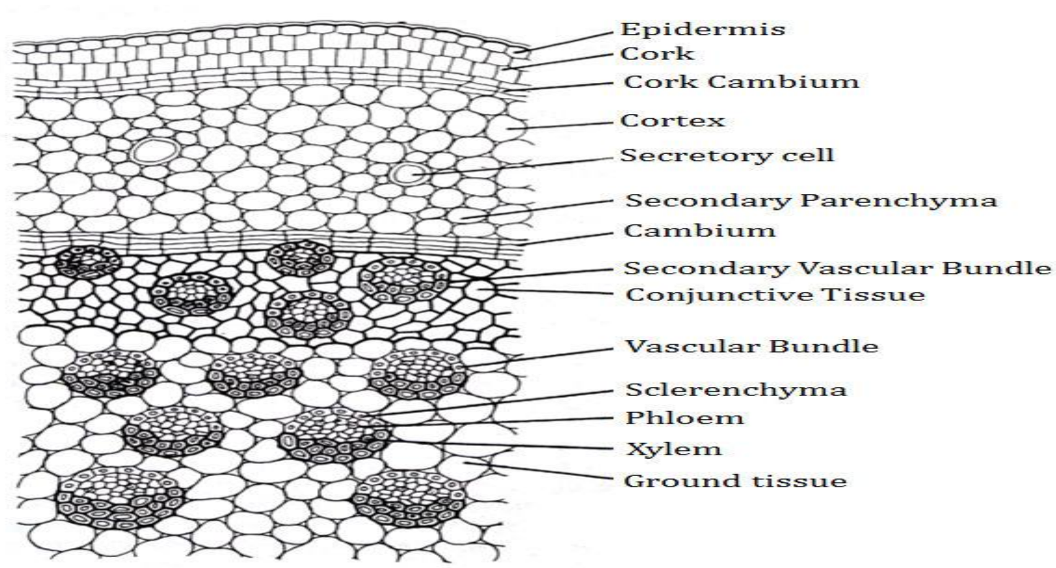


Leptadinia **stem**

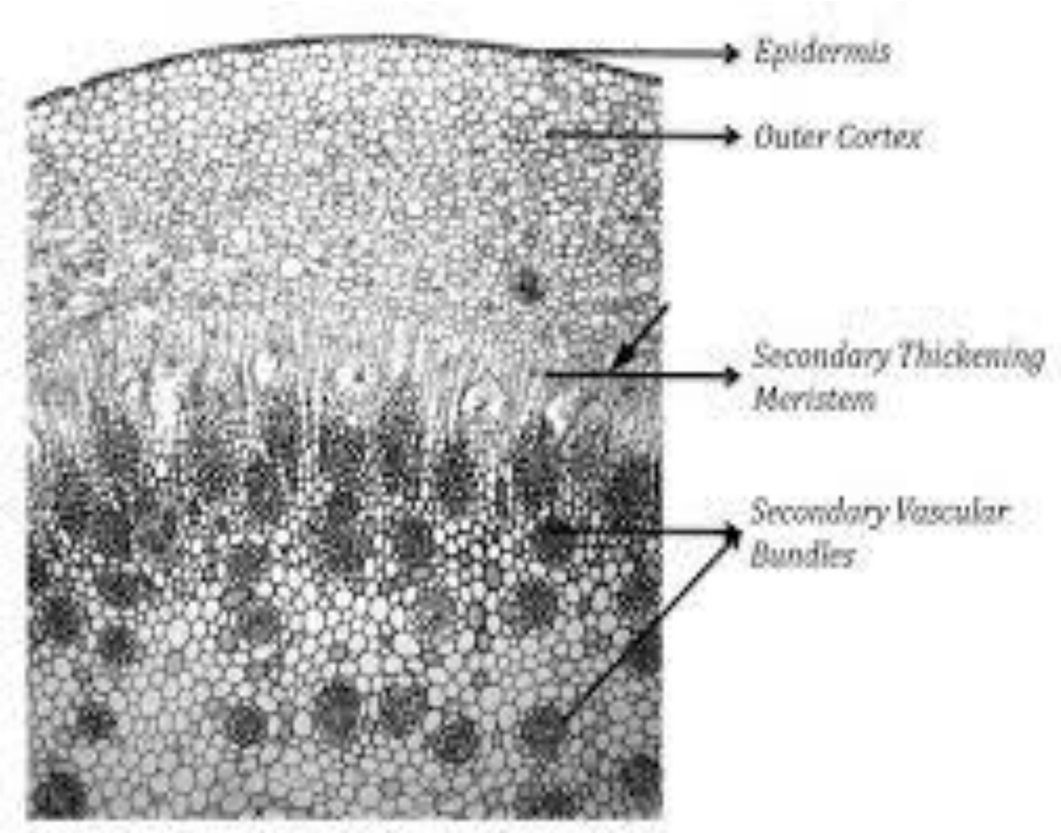
b) Monocot Stems:

Monocots usually lack secondary growth, but may develop thick stems (e.g., **palms**) by primary growth alone. Anomalous secondary growth occurs in some members of liliaceae. The cambium arises in the parenchyma outside the vascular bundles and produce complete vascular bundles and ground parenchyma towards the inside and a small amount of parenchyma towards the outside. In the development of the vascular bundles, individual cells derived from the cambium divide longitudinally. The products of the final divisions differentiate into Amphivasal vascular bundles. They are arranged in radial rows, whereas the primary bundles are located at the center of the stem and are not arranged; but scattered.

Some monocots which showing secondary thickening also develop periderm as the case of the dicots, as for example in ***Aloe*** and ***Dracaena*** stems.



Anomalous Secondary Thickening in *Dracaena (Diagram)*



Anomalous Secondary Thickening in *Dracaena*

SECONDARY GROWTH IN ROOTS

The secondary growth in roots, as in stems, consists of the formation of secondary vascular tissues from a vascular cambium and of periderm from a phellogen. Secondary growth is characteristic of roots of dicots and gymnosperms. It occurs in various amounts in dicots and in some of them the roots remain in primary state during their life. The roots of monocots commonly lack secondary growth.

Common types of secondary growth in roots:

The vascular cambium is initiated by divisions of the undifferentiated cells between the primary phloem and the primary xylem. Therefore, at the beginning, the cambium has the form of strips whose number depends on the type of root. There are two strips in the diarch root, three, in the triarch and 4 in the tertra-arch and so on. After that, the pericyclic cells opposite to the primary xylem become active as a cambium and then the cambium strips become connected together. The cambium located on the inner surface of the phloem begins to divide early than that formed from the pericycle. By formation of secondary xylem opposite to the phloem the cambium is moved outward and finally its circumference becomes circular in cross section.

The cambium produces phloem and xylem cells by tangential divisions and increases in circumference by radial divisions. The cambium arising on the inner surface of the phloem produce conducting elements together with other cells usually present in xylem and phloem. The cambium originating in the pericycle produces ray parenchyma. Rays also appear in the other parts of the 2ry tissues, but those originating in the pericycle opposite to the primary xylem are wider. In some roots, no wide rays are formed, and the xylem appears rather homogenous.

The formation of periderm follows the initiation of secondary vascular growth. The pericyclic cells undergo tangential and radial divisions. The tangential division cause the increase of the number of pericyclic layers in radial direction. The combined increase in thickness of the vascular tissues and of the pericycle forces the cortex outside. The cortex does not undergo an increase in circumference but becomes ruptured and sloughed off together with the epidermis and endodermis. The phellogen arises in the outer part of the pericycle and its cells undergo tangential division, differentiating to phellen (cork) cells centrifugally, and phellodermal cells centripetally. Frequently the number of rows of cork cells is very much greater than phellodermal cells and in some cases only cork is formed. If the phelloderm is formed, it is often difficult to distinguish from the pericycle which increases in growth before the phellogen was initiated and with the phelloderm are referred to as secondary cortex.

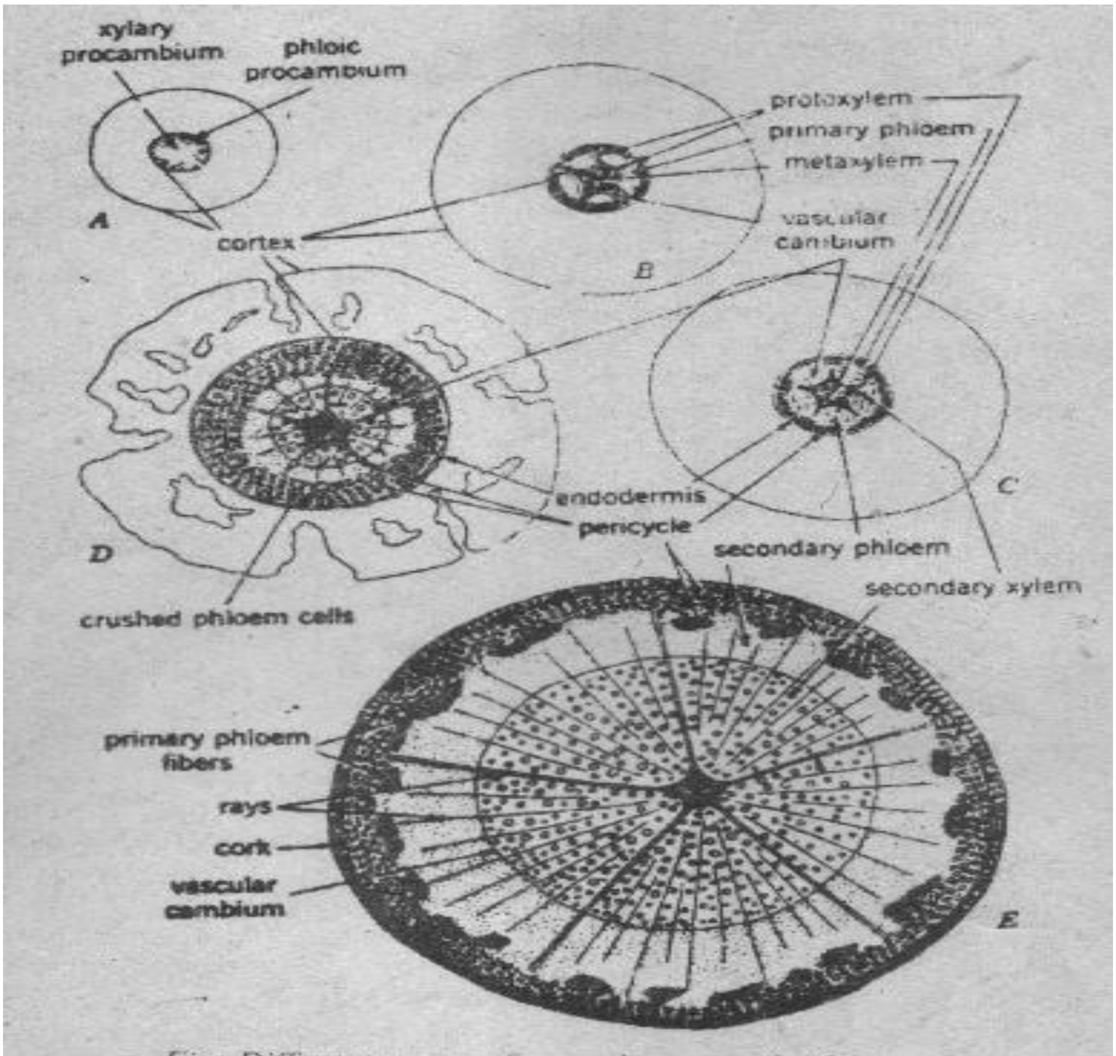


Fig: Different stages of secondary growth of root

TYPES OF ROOTS

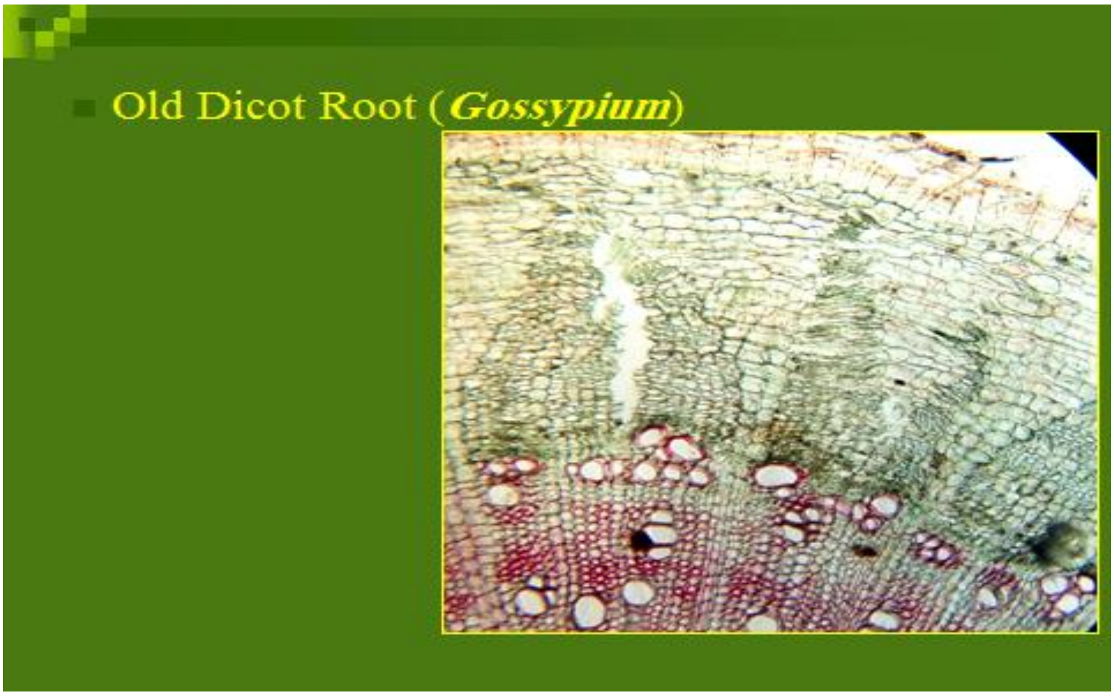
Herbaceous dicots:

Example of secondary growth in herbaceous dicot roots is the case of **Medicago sativa** (alfalfa). The secondary xylem contains vessels of various diameters mostly with scalariform and reticulate pitted walls. The vessels are accompanied by fibers and parenchyma cells. Wide rays of parenchyma divide the xylem into portions. Herbaceous dicots have generally limited amount of secondary growth.

The phloem contains sieve tubes with companion cells, fibers and parenchyma cells, the wide rays of the xylem are continuous through the cambium with similar rays in phloem. The outer phloem contains only fibers and storage parenchyma, and the old sieve tubes are crushed. Periderm is formed from the pericycle as a protective tissue. Superficial periderm (epidermal or cortical) is formed in some species such as **Convolvulus** which in this case retain the cortex.

Woody species:

This type of roots resembles in its anatomical structure those of herbaceous species, but it contains more lignified elements. The roots of gymnosperms are like those of woody dicots except for difference in type of elements consisting the xylem or phloem. Vascular rays are usually narrow, and the secondary growth is homogenous. Periderm usually originates from the pericycle.



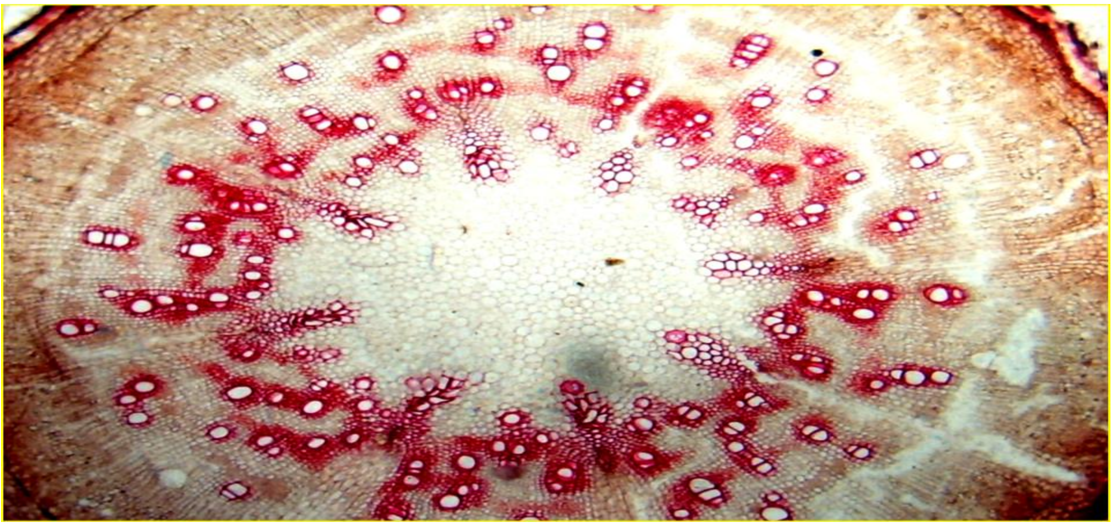
Old Dicot Root (*Gossypium*)

- Old Dicot Root (***Gossypium***)

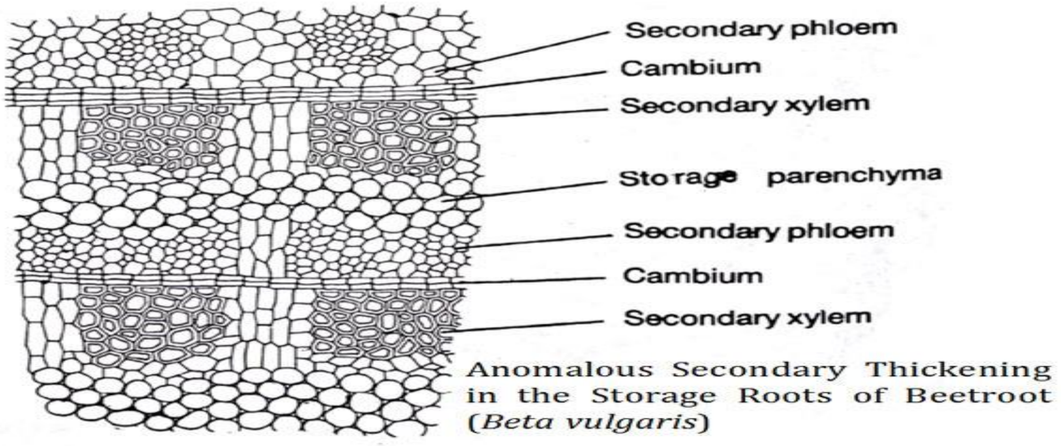
Storage roots:

Several variations in secondary structure occur in storage roots. In roots of **Umbelliferae** as carrot, the secondary growth is of the ordinary type, but parenchyma predominates in xylem and phloem.

In beet, however, the main increase in thickness results from anomalous type of growth. The cambium formed is anomalous in its position and activity. After a short period of secondary growth, the normal cambium ceases to function, and a series of concentric cambial layers arise outside the normal vascular core. The position of each new cambium as it arises in the pericycle is that it encloses few layers of pericyclic cells. These cells increase in number rapidly than the formation of vascular tissues from the cambium. Alternate bands of pericyclic parenchyma and vascular bundles are formed. The pericyclic parenchyma forms the dark colored regions, the vascular bundles bands from the light-colored rings.



■ Abnormal Old Dicot Root (***Beet*** Root)



Anomalous Secondary Thickening in the Storage Roots of Beetroot (*Beta vulgaris*)

In potato root, the xylem contains a large portion of parenchyma which arise in normal manner, Cambia develop in the parenchyma around individual vessels and produce few trachieds toward the vessels and few sieve tubes away from the vessel and many storage parenchyma cells in both directions. A cambium in normal position separates the xylem from the phloem and a periderm is formed from the pericycle.

PERIDERM

The periderm is a protective tissue of secondary origin replacing the epidermis in stems and roots. In plants with primary growth only, such protection is usually given by the cuticle and the cutinization of the epidermis or possibly the hypodermics or outer cortex. In the older stems and roots of most woody plants, however, secondary growth is followed by the rupture and death of the outer tissues and the formation of a new protective layer known as the periderm. Periderm is best seen in woody dicots and gymnosperms. Leaves produce no periderm. Periderm occurs in herbaceous dicots especially in older parts of the stem. Some monocots have periderm.

Structure:

Periderm consists of three layers of tissues, the initiating layer of meristematic cells known as the phellogen or cork cambium, the layer of cells formed by this meristem towards the outside known as cork or phellen, the layer of parenchyma cells formed to the inside known as phelloderm.

a) Cork cambium (phellogen):

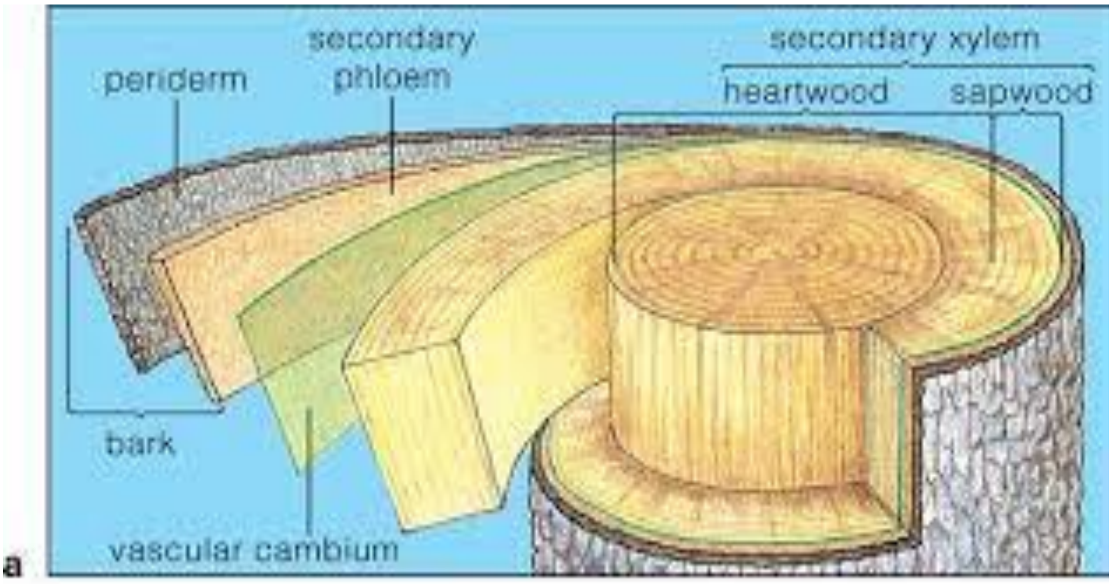
It is a typical example of secondary meristem since it arises by the transformation of permanent cells into meristematic cells. These cells may be epidermal, cortical or phloem cells. It is a lateral meristem since its activity results in an increase of the diameter of the axis (lateral increases). Phellogen cells are isodiameteric or may be radially flattened. It is being first formed as a unisereate layer of initial. This activity always occurs in parenchymatous or collenchymatous cells or in other living cells where they are sufficiently abundant to permit formation of considerable vertical and tangential extent. During the transformation of the parenchyma cell into a meristimatic cell, the protoplast loses their central vacuoles, and the cytoplasm increases in amount and becomes richer and more granular.

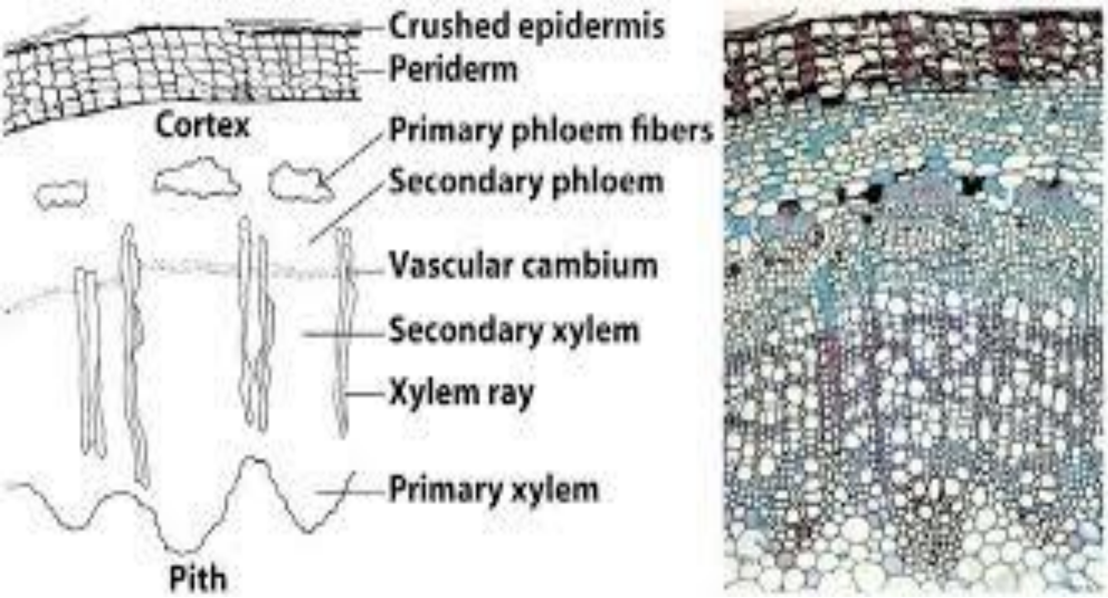
Division of phellogen cells occur in a similar pattern to that of true vascular cambium. The derivatives are arranged in radial rows. The cells formed to the outside differentiate to form dead cork cells, whereas those formed to differentiate their inside to living parenchyma cells or the phelloderm.

Cork:

The cork cells, or called the phellem are, arranged compactly without intercellular spaces in radial rows. The walls are irregular in tangential plane. The walls are suberized in which suberin covers the original primary cellulosic wall which may be lignified. The cells vary in thickness and the walls may be colored brown or yellow. The cells lack cell contents. Mature cork cells are nonliving and usually have no pits in their walls. Different types of cork cells are known.

In the first type, cells are thin-walled, empty and radially elongate, this type is a light tissue which is the beetle-cork type. In other type, the cells are thick-walled and which the lumen filled with dark-staining material of a resinous or tanniferous matter. Sometimes these two types alternate and, in this case, the thin-walled type is easy to rupture than the other type resulting into the split of thin papery sheets. Cork cells may be elastic to a high degree as in **Quercus**, therefore permitting extension, whereas in other species it may be inelastic and inextensible. Phellem prevents water loss from inner tissues due to the suberization of the cell walls.




Crushed epidermis
Periderm
Cortex
Primary phloem fibers
Secondary phloem
Vascular cambium
Secondary xylem
Xylem ray
Primary xylem
Pith

Phelloderm:

They are living cells with cellulosic walls. They are more or less loosely arranged and, in most cases, they are similar to cortical cells. They may function in photosynthesis and may store starch. Sometimes the phelloderm is called 2ry cortex. The phellederm is commonly small in amount, sometimes restricted to the single layer of cells formed on the inner side of the phellogen after the first tangential division. In general cork cells are numerous and are produced from the phellogen each year.

Formation of periderm (origin):

In many species such as **Quercus** super**, Solanum,** the first layer of cork cambium is differentiated in the **Epidermis** itself. In other species the first periderm of a stem originates most commonly in the **Subepidermal** layer such as in **Populus**, **Magnolia**. In this case the epidermis ruptures and disintegrates. In potato tuber, phellogen originate in both **the epidermis and subepidermal** layer. In some species, the first periderm appears rather deep in the stem, usually form deep layers in the cortex. In **Vitis**, periderm first originate from the **primary phloem** and latter in old stems it is followed by another periderm which originate from deeper tissues (**secondary phloem)**.

The first phollogen is initiated either uniformly around the circumference of the axis or in localized areas or overlapping layers. The latter formed periderms appear as discontinuous and overlapping layers. The formation of each periderm layer prevents all tissues to the outside from obtaining food and water, so that all the tissues outside the periderm dies. As a result, layers of successive and overlapping layers of cork enclosing peckets of dead cortical or phloem tissue. These tissues make up the rhytidome often called shell bark and scale bark.

The term bark is used to describe all the tissues outside the vascular cambium. It includes secondary phloem, the primary tissues that may remain, the periderm and the dead tissues outside the periderm. The death of cells outside the periderm, makes the types of bark, the outer nonliving bark, and the inner living bark. The phloem is the innermost parts of the living bark.

In roots deep periderm formation occurs. The phellogen usually originate from **the pericycle.** The dead tissues outside the periderm usually decay in the soil and do not remain adhering to the root. In many herbaceous roots no periderm is formed, but the superficial layers become suberized.

In herbaceous monocotyledons, a persisting epidermis with its cuticle and cutinized walls is usually the protective layer. When this is weakened or ruptured, the primary cortical cells beneath become suberized as in typical cork cells. This occurs commonly in Gramineae and other families.

In many monocotyledons, with secondary thickening for example, **Dracaena** and some species of **Aloe**, the protective layer is formed of **storied cork**. This type of cork differs from typical periderm in origin and arrangement of its radial rows of cells. In the storied cork, the initials-primary cortical cells lie in an irregular line, and each divide to form 3-8 layers of cells. Tangential bands of these cell rows form “stories”. The bands are irregular in outline and indefinite in extent.

Function of periderm:

Protection is the principal function of the periderm. In fruits periderm may replace the heavily cutinized cells as in potato. They also function in support and preservation of the tissues from unfavorable environmental conditions. Cork lay when of considerable thickness may serve for protection against mechanical injury to the tissues beneath them.

Lenticels:

A lenticel may be defined as a limited part of the periderm in which the phellogen is more active than elsewhere and produces a tissue which in contrast to phellen has numerous intercellular spaces. The lenticel phellogen itself also may have intercellular spaces. Because of the presence of intercellular spaces, the lenticels are supposed to be structures permitting the entry of air through the periderm.

Lenticels are usual components of periderm of stems and roots. It appears as a mass of cells that protrudes above the surface of the periderm. It varies in size form structures barely visible to 1 cm. and more in length.

The phellogen of the lenticel is continuous with that of the periderm but usually bands inward so it appears more deeply situated. The loose tissue forming the lenticel is the complementary tissue, the tissue formed toward the inside is the phelloderm.

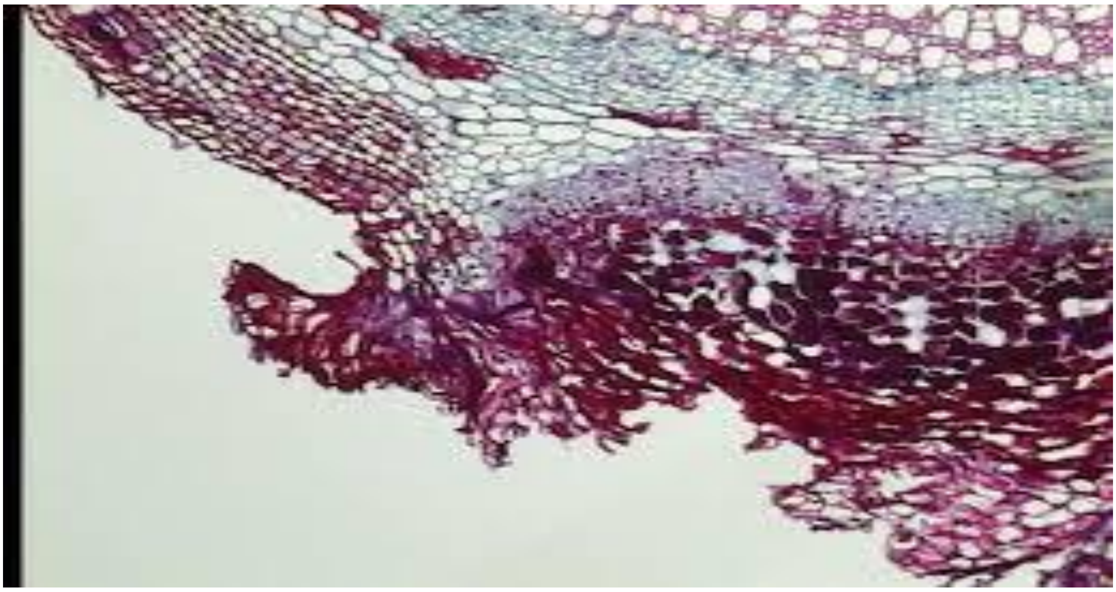
In gymnosperms the complementary tissue cells are like that of phellem except for the presence of intercellular spaces and thinner walls.

In dicot three structural types of lenticels are present:

1- Exemplified by species of **Clerodendron**, **Malus**, **Populus**, **Pyrus** **Salix** has a complementary tissue composed of suberized cells but with intercellular spaces.

2- The type found in **Quercus**, **Sambucus**, **Tilia** consists mainly of a mass of loosely no suberized complementary tissue succeeded by a more compact layer of suberized cells.

3- The type found in **Prunus** shows the highest degree of specialization. The complementary tissue is layered because loose no suberized tissue alternates regularly with compact suberized cells. The compact tissue are the closing layers, which may be broken by new growth.



T.S in lenticel

References

ALLEN, G. S. 1947. Embryogeny and the development of the apical meristem of Pseudo Isuga. HI. Development of the apical meristem. Amer. Jour. Bot. 34: 204-211.

BAILEY, L W. 1930. The cambium and its derivative tissues. V. A. reconnaissance of the vacuome in living cells. Ztschr. f Zelforschung u. Mikroskop. Anatomie 10: 651-682.

BALL, E. 1941. The development of the shoot apex and of the primary thickening meristem in Phoenix canariensis Chaub. with comparisons to Washingtoniafiliera Wat_s. and Trachycarpus excelsa Wend!. Amer. Jour. Bot. 28: 820-832.

BALL, E. 1946. Development in sterile culture of stem tips and subjacent regions of *Tropaeolum majus* L. and of *Lupinus albus* L. Amer. Jour. Bot. 33: 301-318.

BALL, E. 1947. Isolation of the shoot apex of *Lupinus*. Amer. Jour. Bot. 34: Supp. 1a-2a. BALL, E. 1960. Cell divisions in living shoot apices. Phytomorphology 10: 377-396.

BLOCH, R. 194.1. Wound healing in higher plants. Bot. Rev. 7: 110-146. BaKE, N. 1-1. 1941. Zonation in the shoot apices of *Trichocereus spachianus* and *Opuntia cylindrica* . Amer. Jour. Bot. 28: 656-664.

BaKE, 'N. H. 1947. Development of the adult shoot apex and ftoraLinitiation in' *Vinca rosea* L. Aer: Jour. Bot. 34: 433--439.

BUVAT, R. 1944. Recherches sur la dedifferenciation des cellules vegetales. I. Plantes entieres et boutures. Ann. Sci. Nat., Bot., Ser. 11, 5: 1-130. BUVAT R. 1945. Recherches sur .la dedifferenciation des cellules vegetales. II. Cultures de.tissus et tumeurs. Ann. Sci. Nat., Bot., -Ser.-11, 6: 1-119.

CLOWES, F. A. L. 1953. The cytogenerative centres in roots with broad columellas. New Phytol. 52: 48-57.

CLOWES, F. A. L. 1954. The promeristem and the minimal constructional centre in grass root apices. New Phytol. 53: 108-116.

Fahn A. 1969. Plant anatomy 1st edition

Part II

Plant physiology

Chapter 1

Absorption of Water

Water

Life originated in an aqueous environment and in the course of evolution became fully dependent upon water in a number of ways. In general, water is essential for life and its importance to plants may be summarised as follows:

(1) Water is the main constituent of the protoplasm comprising up to about 90 to 95 %of its total weight. In the absence of water, protoplasm becomes inactive and is even killed.

(2) Different organic constituents of plants such as carbohydrates, and proteins, nucleic acid and enzyme etc. , lose their physical and chemical properties in absence of water.

(3) Water participates directly in many metabolic processes. Interconversion of carbohydrates and organic acids depends upon hydrolysis and condensation reactions.

(4) Water increases the rate of respiration. Seeds respire fast in presence of water.

(5) Water is a source of hydrogen atom for the reduction of carbon in the reactions of photosynthesis.

(6) Water acts as a solvent of and carrier of many substances. It forms the medium in which several reactions take place.

(7) Water present in the vacuoles helps in maintaining the turgidity of cells, which is a must for proper activities of life. The turgidity of cells help s in

the elongation of cells resulting in growth. The difference in the amount of available water during summer and winter season for the formation of annual rings in the higher plants. In summer, the turgidity is less and as a result smaller cells are formed.

(8) A network of thin layer of water surrounding each cell plays an important role in the entry and movement of dissolved substances.

(9) Water helps (I) in the transactions of solutes , (II) in the mobility of gametes , (III) in the dissemination of spores , fruits and seeds , and (iv) provides support to aquatic plants .

(10) In tropical plants, water plays a very important role of thermal regulation against high temperatures. Some people think the plants lose about 95 per cent of the absorbed water just to maintain the optimum temperature.

(11) Thousands of characters develop for balancing the water content of planes. Even atmospheric moisture affects plants growth. Different plants absorb water from their general surface while in higher plants roots are the organs concerned with absorption of water.

Soil water

Plants absorb water from the soil by their roots. The water is found in different forms in the soil. The chief source of water to the soil is rain or irrigation. After a rainfall or irrigation some of the water penetrates downwards, under the influence of gravity until it reaches the water table. This is called “the gravitational water” and it is of little benefit for the plants. Moreover, it may be injury to plants. Because it replaces the air between the soil. A major portion of the water is retained by the soil particles against the force of gravity which keep the soil moist. Some of this water is adsorbed by the soil colloids and is held tightly by them in very thin films. This called the “hygroscopic water” and it is non- available for the plants. Another portion of water fills the spaces between the soil particles and called the “capillary water” which is the greatest important for the plants, because it easily absorbed by root hairs. A portion of the gravitational water rises by capillarity and becomes ready available to plants. This portion depends on the structure of the soil, which is generally depend on the size of the soil particle. As soils with relatively small particles held more capillary water than that of relatively large ones.

Movement of water in the plants

1. Absorption of water (root system)
2. Ascent of sap (shoot system)
3. Loosing of water (transpiration) (leaves)

Water absorbing parts of plants

Major portion of water required by plants is absorbed by the roots, but the absorption of water by leaves and stem has also been found in a few plants hydrophytes absorb water by general surface.

The uptake of water by leaves is influenced by:

(i) Structure and permeability of cuticle and epidermis,

(ii) The hairiness of leaf surface,

(iii) The case of wetting surface, and

(iv)The internal environment of deficiency of water in parenchymatous cells closes to the epidermis

Roots play the principle role in absorption of water. Even orchids absorbing water from atmosphere develop modified roots for the purpose.

ROOTS

Roots absorb water mainly from the apical region. Apical organization of root shows three clear demarcations, the zone of elongation and the zone of absorption or differentiation.

The zone of differentiation consist of three different types of tissue system, i.e. dermal, cortical and stellar. Dermal tissue include surface layers of cells. Epidermis in the region has enormous number of unicellular root hairs. Cortical tissue system is complex and consists of pericycle, phloem and xylem etc. Important ones are described here.

Root hair

Root hair is the special modified cell of epidermis meant for the absorption of water. It is specialised not only in appearance but also in its internal structure. The wall of root hair consists of cellulose and pectic substances have great capacity of water absorption.

The cell wall act as permeable layer. Next to cell wall is plasma membrane enclosing cytoplasm, nucleus and vacuole. Vacuole is quite large in size so as to give peripheral arrangement of cytoplasm. The role of vacuole during absorption of water is just like a controller.

MECHANISM OF WATER ABSORPTION

Entry of water in root hair

Root hair maintains contact with soil water and in nature it acts as a soil water –absorbing organ. The water diffuses in to the root hair as a result of diffusion pressure deficit (DPD) gradient. The cell sab contains a more concentrated solute than the water present outside.

Water enters as long as DPD of cell sap is greater distending the cell until the elasticity, of stretched wall is sufficient to balance the osmotic pressure of solutes.

How exactly water enters in the root hair and what is the precise mechanism of water absorption have been explained by two different approaches.

(i) Active absorption.

(ii) Passive absorption.

Active absorption

When we speak about water being absorbed actively, we mean that water is being absorbed through expenditure of metabolic energy. Active absorption occurs as a result of activities in root and does not concern the shoot. Generally it is thought that the active absorption of water may occur in one of two ways, as a result of the active absorption and accumulation of salts or through non-osmotic mechanisms.

a) **Osmotic active absorption:** actually water absorbed by osmosis and this means that it is does not directly require an expenditure of energy. Water is thought to move from the soil to the interior of root along an increasing osmotic pressure gradient. That is water moves through the root epidermis, cortex, and into the xylem ducts because of increasing solute concentrations as it passes from the exterior to the interior cells of the root. The water absorbed by this manner does not directly require an expenditure of energy. The energy is expended in the absorption and accumulation of salts.

(b) Non-osmotic active absorption: Thimann (1951) and Kramer (1959) suggested that the absorption of water is an active process but occurs due to non-osmotic reason even against diffusion pressure gradient. The process requires an expenditure of energy obtained from respiration. How is the energy utilised is not well explained. It may be used directly.

Following are supporting points of this theory that water is absorbed non-osmotically and there is participation of energy (respiration):

(1) Wilting of roots occurs in non-aerated soils such as flooded areas. It indicates that water is absorbed by living cells under aerobic atmosphere.

(2) Use of respiratory inhibitors such as KCN, reduces the rate of water absorption and exudation from the cut end of stems. Thus, there is some correlation between the processes.

(3) The occurrence of distinctive diurnal variation in water uptake and root pressure. It is faster during day time and slower during night. This fact is also true for respiration.

(4) The water absorption is also influenced by hormones such as auxin. Low auxin concentration increases water uptake and exudation.

(5) The process of absorption occurs in living cells.

Passive absorption

This theory explains that the forces responsible of absorption of water into the roots are governed by other cells. The governing force originates in the cells of transpiring shoots rather than in root itself. This forces develop due to transpiration. With the occurrence of transpiration, the DPD of leaf cells increases, which results in the movement of water from the xylem cells to adjacent mesophyll cells. Due to presence of continuous column of water from leaves to roots through xylem channels, the deficit is transmitted to the xylem of roots and finally to root hairs along which radial movement of water takes place and puts these cells under tension.

Path of Water

We should by now be familiar with the tissues encountered by water moving from the soil to the leaves of plant. In figure 7.8 the path of water through a plant is diagrammatically shown. Water is first absorbed from the soil by root hairs and other epidermal cells in or near the root hair zone. Water then move through the cortex tissue and across the endodermis and pericycle and finally into the xylem ducts. The xylem tissue of the roots connects directly with the xylem tissue of the stem. The xylem of the stem, thus allowing water to move out of the root and into the stem, the xylem of the stem is divided and subdivided many times to form a complex network of water–conducting tissues, finally ending in the fine veins of the leaf. Water moves from the leaf veins into the mesophyll cells, is evaporated from their surfaces, and finally moves as water vapour through the stomates into the surrounding atmosphere.

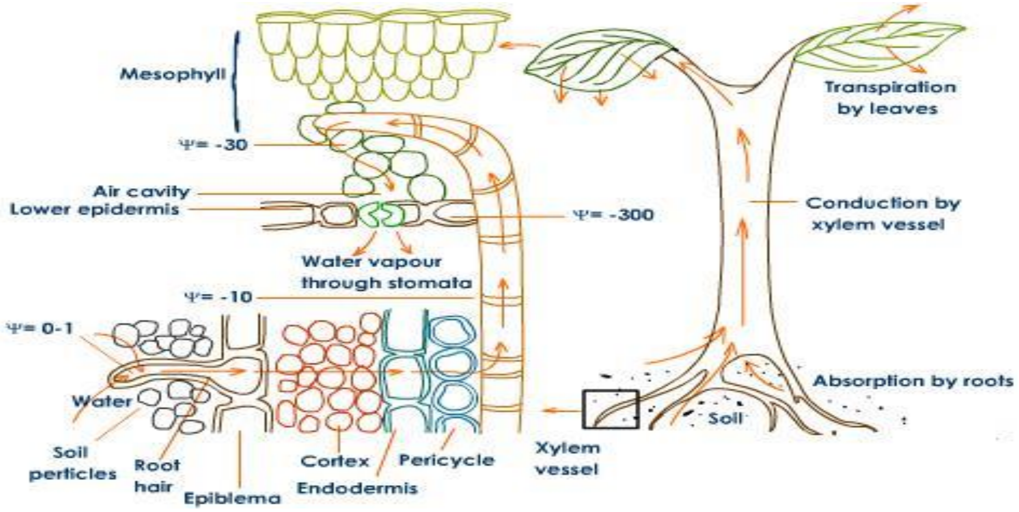


Figure 7.8

Movement of water through plants

Ones the water entered in root hair, it moves first to root stele and then to leaves passing through the different parts of the plant. The movement of water inside the plant shows two different directions. In the first stage, it moves from the root hairs to the stellar region of root via cortex and endodermis, i.e. radial movement of water,

And in the second stage, it moves from the root stele to the top of leaves i.e. upward movement of water. The upward movement is popularly known as “A SCENT OF SAP”

Radial movement of water: (movement of water from root hair to stele):

There are two ways of radial movement of water:

(1) Cell to cell movement of water across the root (osmotic flow).

(2) Movement of water across the cortex along the water filled spaces into the cell walls forming a continuous system from soil water film to endodermis.

Both this mechanisms operate together and help the water to reach up to endodermis.

As a result of the absorption of water from the soil, the root hair cell becomes fully turgid, it is osmotic pressure falls due to dilution and its turgor pressure increased. As a consequence, its suction pressure will fall below that of the adjacent cortical cell **B** as a result water will pass from **A** to **B**.(**Fig. 2).**

The diffusion of water in to **B** likewise reduces its suction pressure which falls below that of the next cortical cell **C**, with the result that water passes from **B** to **C**. in the same manner water pass from the cell **C** to **D**, and from **D** to **E**, from **E** to **F** and from there in to the endodermal cell **N**. from here it is passed on to the pericycle cell **O** which will eventually become turgid. It will then exert no suction pressure and hence, will readily give up water to the xylem vessel with which it is in contact. The walls of the xylem vessel are in elastic so, that there is not turgor pressure and the whole of the osmotic pressure of the xylem sap constitutes its suction pressure. This being higher than the reduced suction pressure of the parenchyme (pericycle) cell **O**, water will draw in to the xylem vessels.

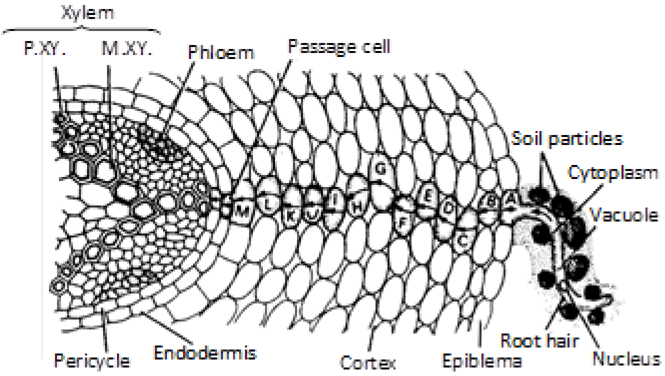


Fig. 2 diagram indicated the movement of water (radial movement) after absorbing from the soil.

FACTOR AFFECTING WATER ABSORPTION RATE

The plant gets two types of environment includes factors such as (a) available soil water , (b) concentration of soil solution , (c) soil temperature and (d) aeration while internal environment includes factors such as (a) transpiration , (b) absorbing root system and (c) metabolism .

External Environmental Factors

(a) Available soil water:

The water in the soil is present in a different forms such as capillary, hygroscopic, gravitational etc, of which capillary water is readily available for absorption. This is in between field capacity and permanent welting percentage where the rate of absorption of water is generally uniform and is not affected. With an increase in water beyond field capacity, aeration of soil is badly affected which reduce s the rate of absorption and under severe conditions wilting results in. The similar wilting is observed in extremely dry soils and a decrease in soil water reduces the rate of absorption.

(b) Concentration of soil solution:

Large number of elements are dissolved in soil water called soil solution. On account of these elements, the concentration of soil solution changes. If the soil solution is highly concentrated, it increases greatly osmotic pressure and when it reaches higher to that of cell sap, water is not absorbed. It is one reason that the plants fail to grow in highly saline fields. This is popularly known as physiological dryness.

(c) Soil temperature

The variation of temperature affect the rate of absorption .20 to 30 °Cis the most suitable temperature for absorption. The low temperature reduces and moderately high temperature increases the rate of absorption. A very high temperature kills the cell. How the low temperature exercises its negative influence in absorption has been explained as follows that it results in:

(I) slower rate of elongation of root thus preventing its contact with areas.

(II) Slower rate of metabolic activities.

(III) Reduce of soil water diffusion into the roots.

(IV) Increased viscosity of water, protoplasts and colloidal gels in the cell wall.

(V) Decreased permeability of cell membrane.

(d) Soil aeration:

Water is absorbed more efficiently in a wall aerated soil than in a poorly aerated soils. Probably the reason may be the respiration as normally roots fail to respire anaerobically and plants shortly die in floated areas. The deficiency of oxygen inhibits the growth and the metabolism and accumulation of CO_2 increases the viscosity of protoplasts and decreases the permeability of cell membrane. Both this factors affect severely and reduce the rate of water absorption. These may be the reasons for plant death in flooded areas. Only few plants such as rice and Typha can grow normally in poorly aerated soils as these are specially adapted to such environments.

Internal Environment Factors

(a) Transpiration.

The rate of absorption of water is nearly directly proportional to that of transpiration. A higher rate of transpiration increases the rate of absorption because of cohesion theory of ascent of sap, i.e. transpiration produces a tension or pull, transmitted to roots through hydrostatic system of plants creating a favourable condition for entrance of water.

(b) Absorbing root system.

The efficiency of water absorption depends upon the absorbing system. The presence of number of root hairs accounts for the rate of absorption. However, the development of root hairs depends upon environment. The maize plants does not produce root hairs in culture solution but produces large number of root hairs when grown in soil. In moist conditions root hairs are well developed and large in quantity. The coniferous plants (gymnosperms) bear few or no root hairs but absorb large amount of water with the help of mycorhizal hyphae. Thus root systems play a major role in absorption of water

(c) Metabolism.

The metabolism and absorption are closely related. Although doubt exist in use of energy during absorption, but factors inhibiting rate of respiration-such as poor aeration application of anaesthetics and KCN reduce the absorption rate . Thus metabolic activities are expected to participate indirectly by forming a constantly elongated root system and always providing newer contacts with soil water.

Chapter 2

Various elements found in plants

Major elements

Serious attempts to determine experimentally the mineral content of plants were made by **Sachs and knop** as far back as 1860. Using liquid cultures, they were able to show that ten elements are essential to the plant. these they listed as carbon (C) hydrogen (H) , oxygen (O) , nitrogen (N) , Phosphorus (P) , potassium (K) , Calcium (Ca) , Sulfur (S) , Magnesium (Mg) , and Iron (Fe) . These ten elements were generally accepted as all that a plant needed for normal growth and development. However, we know today that there are growth of most plants and several additional elements specifically required by certain plants.

Method of detections

Several of the methods used in the early study of plant nutrition are still in use today. The analysis of plant ash and the use of liquid and sand cultures are techniques used for the study of plant nutrition in laboratories throughout the world. However, these methods have been refined and improved upon.

Ash analysis

A reasonably reliable means of detecting the mineral element content of a plant is to subject the plant to high temperatures (about 600 °C) and then analyse its ash content. Only ten mineral elements are present all of the organic compounds having been decomposed and passed off in the front of gases. These primary elements (carbon, hydrogen, and oxygen) are therefor given off as CO_2, water vapour and oxygen. In addition to carbon, hydrogen, and oxygen, the element nitrogen cannot be detected accurately with this method, since some of it is given off in the form of ammonium or nitrogen gas. All of the other mineral elements that were absorbed from the soil are present in plant ash.

Although the analysis of plant ash may be thought of as a method of determining the relative quantities of mineral elements in a plant, it is, at best, a crude technique. Too many variables are present to give accurate, reliable results. For example, vaporization or sublimation of some of the elements may be caused by the high temperatures. Generally, elements are not present in pure state in the ash, but are in the form of oxides. finally , the qualitative and quantitative analysis of the ash for the different elements present is depended on different chemical treatments the accumulative error resulting from this facts quantitative data obtained from the ash analysis of plant tissue.

Solution cultures

It did not take scientists long to realize the impracticality of using soil as a medium for growth in any serious study of plant mineral requirements. To render a soil free of the mineral elements used by plants and then control the amounts of nutrients made available to the roots imbedded in the soil is impossible. On the other hand, solution cultures provide an excellent means for controlling the quantity and relative proportions of minerals salts given to a plant in any of one experiment. Two other good reasons for using solution cultures in mineral nutrition studies are the excellent solvent characteristics of water and the relative ease with which water can be freed of most contaminating influences.

Good quantitative studies may be made of the nutritional need of plants using water as a medium. However careful attention to small details is necessary to achieve good results. Due to the fact that satisfactory growth may be achieved with extremely small amounts of trace elements, contamination problems are always present. Some of the sources of the contamination are the rooting medium, reagents used containers, the water, cutting implements, seeds and the dust in the surrounding atmosphere. Obviously, total elimination of these contaminating influences is impossible, but they can be kept to a minimum.

Several studies have shown that the best container for solution cultures are made of borosilicate grass or natural polyethylene **(Hewitt, 1963)**. However, even with the use of these materials, some contamination may be expected, such as the presence of boron in borosilicate glass and, perhaps, molybdenum and cobalt in polyethylene. Water distilled in metal stills usually is contaminated with trace amounts of copper, zinc, and molybdenum. Redistillation of water in stills made entirely of borosilicate glass is necessary to remove this elements **(Piper, 1942; Ston and Arnon, 1939)**. Another satisfactory method of ridding water of contaminating trace elements is to pass it over cation and anion exchange resins **(Hewitt et al., 1954).**

In early studies of plant nutrients reagents used presented a major source of contamination. These reagents had to be purified by various means before trace elements deficiencies could be demonstrated. Reagents may be purchased today that are pure enough for most studies. But even this contain trace amounts of contaminants.

From the discussion above, one can see that most of difficulties encountered in mineral nutrition studies are associated with trace element contamination. A study of deficiencies caused by major nutrients can be easly accomplished because of the relatively large amounts needed for normal growth. Here, a small amount of contamination is not a serious problem.

With proper attention given to the problems discussed above, the next step is to prepare stock solutions from inorganic salts containing the necessary elements for normal plant growth. Once stock solutions are prepared and the proper containers obtained and filled with deionized water, nutrient solutions may be prepared by simply adding, in the correct proportion, the necessary inorganic salts from the stock solutions. Several satisfactory formulas for nutrient solutions have been prepared.

Sand cultures

Solid media, such as sand or crushed quartz, are generally easier to work with than a liquid medium. On the other hand, purification problems are more difficult to cope with. However, today it is possible to purchase highly purified silica sand or crushed quartz that is very low in available trace elements. The added attraction a solid culture is that the roots are growing in a nature medium and no means of support needs to be provided. Nutrient solutions are added to the solid culture by three different ways: pouring over the surface (slop culture), dripping on the surface (drip culture), and forcing solution up from the bottom of the container (subirrigation). In the all three systems, the nutrient solutions added drain out through an opening in the bottom of the container. In subirrigation, the system may be attached to a timing mechanism, which may be set to give periodic irrigation to the sand.

Of the three methods, the slop culture is the easiest to manipulate, but offers the least control. The drip culture may be set up so that the amount of solution being added equal to the amount of solution draining off. This method allows for continuous nutrients supply and partial control of the amount of nutrients reaching the root system. The last system, subirrigation, may be set up to work automatically and also gives partial control of the amount of nutrients reaching the plant roots. The subirrigation system is the most desirable of the three systems, but the hardest and most expensive to set up initially.

Chapter 3

Occurrence of the various elements

Because of their relative importance and abundance in the plant carbon, hydrogen, oxygen, and nitrogen will not be covered in this chapter but will receive more extensive attention in separate chapters**.**

Phosphorus

Phosphorus is present in the soil in two general forms, inorganic and organic. In the organic form, phosphorus may be found in nucleic acid, phospholipids, and inositol phosphates, compounds common to the organic fraction of the soil. To the author's knowledge, there have been no reports of plants absorbing organic phosphorus, either from the solid or solution phase of the soil. Therefore, organic phosphorus represents an unusable form of the element with respect to the plant. However, organic compounds are eventually decomposed and phosphorus is released in an inorganic form, which is readily taken up by the plant.

Much of the phosphorus of the soil solution is present in the inorganic form, mainly as the phosphate ions $H_2PO_4^-$ and HPO_4^{2-} (wiklander, 1958). The quantity of either ion present is dependent upon the PH of the soil solution, the lower pH favouring the H_2PO^{4-} ion and the higher pH, HPO_4^{2-}.

Calcium

Generally, calcium is the major exchange cation of fertile soils (**marshall, 1951**) .However, the major portion of calcium in the soil is found in a nonexchangeable form, chemically bound in primary minerals such as anorthite ($CaAl_2Si_2O_8$). Through a weathering, this calcium can be made available. We have already mentioned the presence of calcite ($CaCO_3$) of soils in semiarid and arid regions and the general occurrence of insoluble calcium is available to the plant, depending upon the solubility of the salt and the degree of alkalinity.

Liming

The most effective and economical method of controlling soil pH is the application of the lime. lime to the chemist is calcium oxide (CaO) , but to the farmer , it is any compound containing calcium or magnesium capable of counteracting the harmful effects of an acid soil **(Millar et al ., 1951) .**

In an acid soil, we have clay micelles with a predominance of exchangeable hydrogen ions absorbed to their surfaces. With the addition of lime compounds, such as calcium carbonate ($CaCO_3$) or calcium oxide (CaO) many of hydrogen ions are replaced by calcium ions. In addition, the released hydrogen ions are tied up in the form of water. The final result is a rise in pH and an increase in the supply of exchangeable calcium ions (figure 13-4).

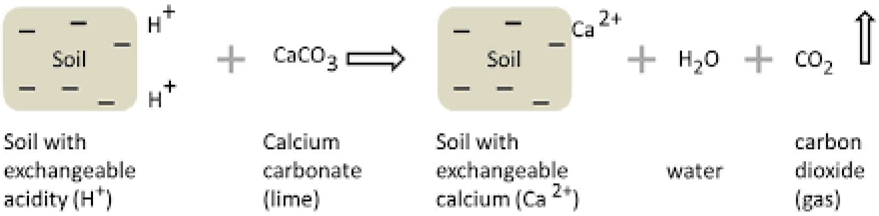


Figure 13-4

One should be cognizant of the harmful effects of liming, as well as the beneficial effects. Over liming a soil may cause the pH of the soil to rise above 7.

Magnesium

Magnesium is present in the soil in water-soluble exchangeable and fixed form and is present in primary minerals (**Bould, 1963**).

Magnesium in minerals such as magnesite ($MgCO_3$) , olivine ($MgCO_3)_2SiO_4$) , and dolomite (MgCO3 .$CaCO_3$)is available to plants in satisfactory amounts for growth .

Potassium

Potassium is present in the soil in a nonexchangeable or fixed form, an exchangeable form, and a soluble form. Although there is a relatively high content of this element in the soil, most of it is nonexchangeable and, therefore unavailable to the plant.

When we speak of an element being unavailable, especially with respect to potassium, we mean that utilization of the element in its present form by the plant is not possible. However, availability of potassium in potassium-bearing minerals, such as biotite, muscovite, and illite , is made possible through normal weathering processes .

An equilibrium exists between the soluble, exchangeable, and fixed forms of potassium

Soluble K == exchangeable K == fixed K

Sulfur

Soil sulfur is found primarily in the organic fraction (**Quastel, 1963**), but may also be found in minerals such as pyrite, cobaltite, gypsum, and epsomite and in the soil solution as the sulfate ions $(SO_4)^{2-}$. Sulfur is the phosphate ion, the sulfat ions is weakly adsorbed, the adsorption increasing with a decrease in soil pH. Adsorption is favoured by the presence of hydrated oxides of iron fate ion is generally thought of as replacing hydroxyl ions in clay minerals , a process known as anion exchange.

Organic sulphur is made available to the plant through biological oxidation. Through the activity of certain microorganisms, sulfur is transformed from the organic form to the sulfataion, the form of sulphur that higher plants absorb. Not only do soil microorganisms oxidize organic sulphur, but also sulphide minerals, such as ferrous sulphide (FeS). Where there is good aeration, moisture and suitable temperature, FeS canbe chemically oxidized to elemental sulfur.

The elemental sulfur is then oxidized sulfate by sulfur bacteria. The two-step oxidation of ferrous sulphide in soil was first demonstrated by **Wiklander et al. (1950).**

And may be written as follows:

$$FeS + H_2O + \frac{1}{2} O_2 \rightarrow Fe(OH)_2 + S$$

$$2S + 2H_2O + 3O_2 \rightarrow 2H_2SO_4$$

Biological oxidation in the soil of pyrite (FeS_2) has also been demonstrated, sulphuric acid being the final product **(Wiklander, 1958)**

Another source of soil sulfur is the atmosphere, the sulfur being brought to the soil by rain and snow.

Iron

Soils generally are not deficient in iron, but may be deficient in exchangeable and soluble forms of iron. Appreciable quantities of iron are present in minerals in hydrated oxides such as limonite ($Fe_2O_3.3H_2O$), and in the sulfide form (**Bould, 1963**). Iron is most available to the plant in the ferrous form, but significant quantities of the ferric ion may also be absorbed.

The availability of iron to the plant is controlled rather sharply by the soil pH. In acid soils, appreciable amounts of iron are dissolved in the soil solution and available to the plant. However, in neutral or alkaline soils, iron is much more insoluble. In fact, one of the dangers of overliming is that the resulting increase in pH will cause symptoms of iron deficiency to appear on plants. However, even in soils poor in soluble iron, this element may be available by the direct contact of plant roots with iron-containing soil particles **(Chapman, 1939).**

Manganese

According to **Leeper (1947)**, the manganese of the soil may exist in the bivalent, trivalent, and / or tetravalent forms. The bivalent ion may be found dissolved in the soil solution or as an exchangeable ion adsorbed to the soil colloids, both of which are available to the plant. The exchangeable bivalent ion is significant in manganese nutrition, since very little of the soil manganese is likely to be found dissolved in the soil water **(Stiles, 1961).**

Copper

The major portion of the copper of primary rock is present as chalcopyrite ($CuFeS_2$), which is the probable source of natural deposits of copper sulfide in the soil **(Bould, 1963).**

The divalent copper cation is adsorbed very strongly to the soil colloids and organic materials of the soil **(Hasler, 1943)** a form of which it is relatively exchangeable. adsorption of copper as a complex monovalent ion ($CuOH^+$, $CuCl^+$) has been demonstrated in organic soils **(Llucas , 1948**) and on clay minerals **(Menzel and Jakson , 1950) .**

Zinc

According to **Bould (1963)**, zinc occurs in the ferromagnesium minerals, magnetite, biotite, and hornblende. Weathering of these minerals releases zinc in the divalent form, which is readily adsorbed onto soil and organic matter in exchangeable form.

As with many other essential elements, one of the factors controlling the availability of zinc is the soil pH. The availability of zinc decrease with increase in pH, making it very likely that symptoms of zinc deficiency may occur in plants growing in alkaline soils.

Boron

Boron appears in exchangeable , soluble , and nonexchangeable forms in the soil , that is , as boric acid (H_3BO_3) , calcium or manganese borates , and as a constituent of silicates **(Bould , 1963 ;Wiklander , 1958) .** Like zinc, the dissolved boron content in the soil solution is very low.

Molybdenum

According to (**Wiklander, 1958**), molybdenum is present in soils in three forms:

- dissolved in the soil solution as molybdate ions (MoO_4^{2-} or $HMoO^{4-}$),

- adsorbed to soil particles in an exchangeable form,

- In a nonexchangeable form as a constituent of soil minerals and organic matter.

Chapter 4

Phosphorus

Function

- Phosphorous is found in plants as a constituent of nucleic acids and nucleoprotein so, it is found in the meristematic regions with higher concentration.
- It is found as a constituent of phospholipids which form the cell membrane.
- Also, it is found as a constituent of the coenzymes NAD and NADP that are important in oxidation reduction reactions in which hydrogen transfer takes place.
- In addition, Phosphorous is found in the most important constituent ATP which acts as an energy transfer compound.

Deficiency symptoms of phosphorus

1-Falling of the premature leaves.

2- Formation of purple or red anthocyanin pigmentation.

3-Developing of dead or necrotic areas on the leaves, petioles or fruits.

4-With more severe deficiency, leaves turn pale brown and die, and roots may turn dark and discolored in sorghum

5- Stunted growth.

6-Sickle leaf disease is caused in P deficiency, which is characterised by chlorosis adjacent to main veins followed by leaf asymmetry.

Nitrogen

Function

- Nitrogen has an important role as it found in the structure of protein molecule
- It is found in such important molecules as purines, pyrimidines and prophyrines.
- Purines and pyrimidines are found in the nucleic acids, DNA and RNA which are essential for protein synthesis.
- The prophyrines are important for the metabolism of some compounds such as chlorophylls and the cytochrome enzymes.

Deficiency symptoms of nitrogen

1-the chlorophyll content of the plant leaves is reduced which results in pale yellow color.

2-young leaves are pale as the older leaves are yellow and drop early

3- Purple color formed on leaf, petioles and vines of tomato as a result of production of anthocyanin pigment.

4-Reduction in cell size and cell division

5-low of nitrogen availability must cause a decrease in protein synthesis.

6-Reduction in protein results in stunted growth and dormant lateral buds

7- Flowering, fruiting, protein and starch contents are reduced.

8- Shoots are thinner and shorter.

Magnesium

Function

- Magnesium is a constituent of chlorophyll molecule without it photosynthesis would not occur.
- Many of enzymes involved in carbohydrate metabolism require magnesium as an activator
- Magnesium acts as activator for those enzymes involved in the synthesis of nucleic acids (DNA, RNA).
- It has a role in protein synthesis.

Deficiency symptoms of magnesium

1-The first sign of magnesium deficiency is the chlorosis of old leaves which progresses to the young leaves as the deficiency progresses.

2- The low amounts of Mg lead to a decrease in photosynthetic and enzymatic activity within the plants.

3- After prolonged magnesium deficiency, necrosis and dropping of older leaves occurs.

4- Production of smaller fruits.

5- Stem becomes yellowish-green, often hard and woody.

Calcium

Function

- Act as a constituent of cell walls in the form of calcium pectate
- Calcium is important in the formation of cell membranes and lipid structure.
- Calcium has a role in normal mitosis
- It acts as activator of some enzymes.

Deficiency symptoms of calcium

1- Necrosis leading to stunted plant growth

2- Curling of the leaves

3- Reduction of plant height, fewer nodes, and less leaf area.

4- Death of terminal buds and root tips.

5-cell walls become rigid or brittle.

6- The common disease is blossom-end rot of tomato (burning of the end part of tomato fruits.

Potassium

Function

- It has a major role in varies process as respiration, photosynthesis, chlorophyll development and water content of leaves.
- Potassium acts as activator for enzymes involved in protein synthesis.
- Also, it acts as activator for enzymes involved in carbohydrate metabolism.
- It has an essential role in apical dominance in the plants.

Deficiency symptoms of potassium

1-Brown scorching and curling of leaf tips as well as chlorosis (yellowing) between leaf veins.

2- Purple spots may also appear on the leaf.

3- Reduction in plant growth, root development, and seed and fruit development.

4- Potassium deficiency symptoms first appear on older (lower) leaves.

5- Stunted in growth and shortening of internodes.

6- Two common diseases are known **"Rosette** "in beet and carrot, bushy growth or rosette condition develops due to potassium deficiency."**Die back".** In acute deficiency cases, there is a loss of apical dominance and regeneration of lateral buds and bushy of growth. In prolonged cases, die back of lateral buds are also resulted.

Zinc

Function

- It participates in the metabolism of plants as an activator of several enzymes.
- It involved in the biosynthesis of the plant auxin (IAA).
- It plays an important role in protein synthesis.

Deficiency symptoms of zinc

1-An interveinal chlorsis of the older leaves starting in the tips and margins.

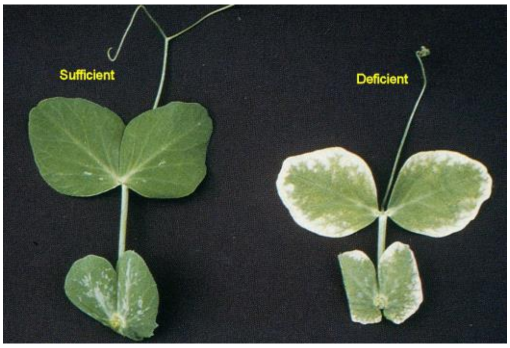
2- White necrotic spots.

3- Seed production and fruits size is greatly reduced.

4- Leaves are often narrower or have wavy margins.

5- Smaller leaves and shortened internodes resulting in stunted growth.

6- The common disease is **little leaf** disease. Yellow mottling of leaves, reduction of leaf size with rosette appearance (due to reduced internodal distance) and die back of the affected branches are symptoms of the disease.



Sulfur

Function

- Sulfur is the constituent of amino acids cysteine, cysteine and methionine
- It also participates in the constituent of vitamin B, co-enzyme A and volatile oils.
- It may be found in sulfhydryl groups, which are present in many enzymes.

Deficiency symptoms of sulfur

1- Sulfur deficiency causes yellowing (Chlorosis) of leaves. Young leaves are affected first.

2- Tips and margins of leaves roll inward.

3- Accumulation of starch, sucrose and soluble nitrogen.

4- Young leaves develop orange, red or purple pigments.

Manganese

Function

- It acts as an activator for enzymes in respiration and nitrogen metabolism.
- It plays an important role in nitrate reduction.
- Manganese thought to be involved in the destruction and oxidation of indol-3-acetic acid (IAA).

Deficiency symptoms of manganese.

1-The leaves start to turn yellow and undergo interveinal chlorosis.

2- The younger leaves near the top of the plant show symptoms first.

3- The chloroplasts of tomato leaves lose chlorophyll and starch grains becoming yellow green in colour.

Copper

Function

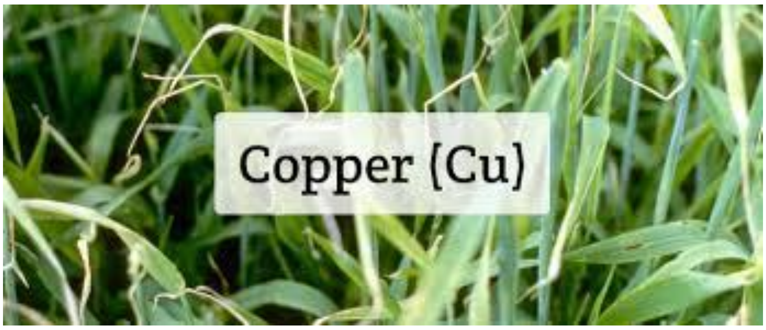
- Copper acts as a component of some enzymes.
- It has a role in photosynthesis process as a constituent of chloroplast.

Deficiency symptoms of Copper.

1-It causes a necrosis of the tip of young leaves that proceeds along the margin of the leaf, giving it a withered appearance.

2- Under sever condition the leaves may be lost, and the whole plant may appear wilted.

3- *Reclamation disease*: It is also called as White Tip disease and is found in legumes, cereals, oats and beet. The tips of the leaves become chlorotic followed by a failure of the plants to set seed.



Iron

Function

- Iron has a number of important functions in the overall metabolism of the plant.
- It appears to be essential for the synthesis of chlorophyll
- It has a major role in the biosynthesis of cytochromes.
- It acts as an activator of some enzymes.

Deficiency symptoms of iron

1- Extensive chlorosis of leaves specially the younger one.

2-The lack of iron may inhibit formation of chloroplasts through inhibition in protein synthesis.

Boron

Function

- Boron has an important role in the transport of carbohydrate within the plant.
- It participates in cellular differentiation, in nitrogen metabolism, fertilization, active salt absorption, hormone metabolism, phosphorous metabolism and photosynthesis.

Deficiency symptoms of boron

1-death of stem and root tips.

2- Abscission of flowers.

3-the leaves may have a coppery texture.

4-leaves sometimes curling and becoming quit brittle.

5- Root growth is stunted.

Molybdenum

Function

- It has an important role in nitrogen fixation and nitrate and phosphorous assimilation.
- It maintain the concentration of ascorbic acid in the plant.

Deficiency symptoms of Molybdenum

1-Chlorotic interveinal mottling of the lower leaves followed by marginal necrosis and infolding of the leaves.

2- Under sever conditions; mottled areas may become necrotic, causing the leaf to wilt.

3-Flower formation is inhibited and if flowers do form, they abscise before setting fruit.

4- A common disease of molybdenum deficiency in cauliflower plants is **whiptail** in which the leaves show an interveinal mottling and leaf margins may become grey and finally brown. The leaf tissues wither, leaving only the midrib and a few small pieces of leaf blade, giving the appearance of a whip or tail.

Chapter 5

Mineral Salt absorption And Translocation

It was thought that osmotically active substances diffused along concentration gradients from soil solution into the plant. The osmotic concentration inside the cell was continuously kept a low point through utilization of the absorbed substances in metabolism. The osmotic theory sufficiently explained the absorption, but did not account for the rapid translocation of the salts once they were absorbed. Again the transpiration stream was implicated, this time as only aiding in the dispersal of the salts, not their absorption. Thus, early attempts to explain salt absorption and mineral nutrition

Translocation only emphasized physical mechanisms, neglecting almost entirely the participation of metabolic energy.

However, during this time, a statement was made by the brilliant physiologist, **Pfeffer**, which contrasted sharply with prevalent theories on salt absorption and remarkably foreshadowed a popular theory today (**Pfeffer, 1900**). **Pfeffer** claimed:

The nature of the plasma is such as to render it possible that a substance may combine chemically with the plasmatic elements, thus being transmitted internally, and then set free again.

This statement agrees very nicely with the carrier theory in salt absorption generally accepted today.

As is usually the case when one tries to buck the tide of popular thought, this provocative theory in absorption was not taken too seriously, and physical mechanisms and models were continuously produced to explain salt absorption. It was finally recognised, from work done in the 1930, that salt absorption is largely dependent upon metabolic energy, that the uptake of salt is predominately active, not passive as was earlier thought.

Passive absorption

Outer and apparent free space

Salt absorption takes place through the intimate contact of the root system with the soil colloids or soil solution. What are the mechanisms involved in the passage of dissolved inorganic salts from the soil solution into the plant? passive or non-metabolic absorption of ions has been demonstrated by numerous investigators (see review by **Briggs and Robertson , 1957**) it has been found frequently that when a plant cell or tissue is transferred from a medium of low salt concentration to a medium of relatively high salt concentration there is an initial rapid uptake of ions this is followed by a slow steady uptake that is under metabolic control . The rapid initial uptake is not affected by temperature or metabolic inhibitors; that is, metabolic energy is not involved. If the above tissue is returned to the low salt medium, some of the ions taken up will diffuse out into the external medium. In other words, a part of cell or tissue immersed in the salt solution is opened to free diffusion of ions. since free diffusion implies that ions can move freely in or out of the tissue , the part of the tissue opened to free diffusion will reach an equilibrium with the external medium and the ion concentration of this part will be the same that found in the external medium .

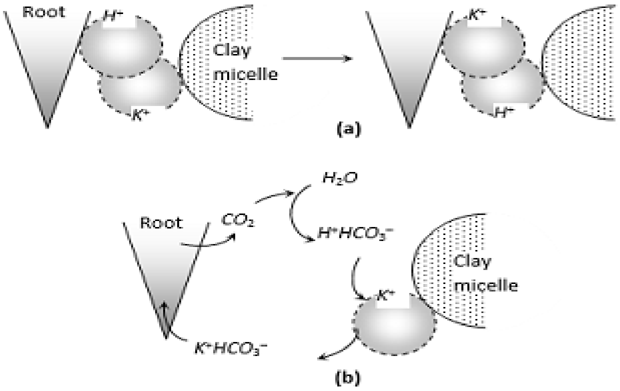
That part of a plant cell or tissue which will allow for free diffusion to take place is referred to as outer space.

With the establishment with the concept of ‘outer space ‘, workers turned to the task of calculating the volume of plant cell or tissue involved. This may be accomplished by immersing a tissue in a solution of known concentration, allowing it to come to equilibrium, and then determining the amount of salt taken up. Assuming that the ion concentration is the same both in outer space and in the external medium and knowing the amount of salt taken up, we can calculate the volume of outer space.

Under the above circumstances, active absorption must be inhibited (e.g., by metabolic inhibitors or by low temperature) or the calculated volume will be greater than the actual volume.

Ion exchange

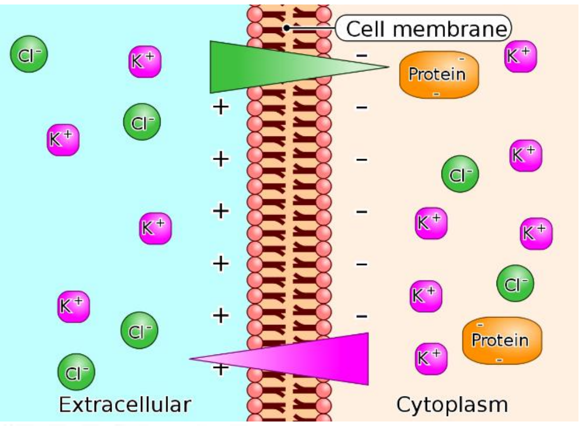
Ions adsorbed to the surfaces of the cell walls or membranes of a tissue may exchange with ions from the external solution in which the tissue is immersed. We have already encountered analogous ion exchange mechanisms between the soil solution and the soil colloids in a previous chapter. Suppose, for example, the cation, K^+, of external solution exchanged with a hydrogen ion, H^+, adsorbed to the surface of the cell membrane. The action would then become adsorbed to the surface of the membrane and rendered osmotically inactive. Anions could exchange with free hydroxyl ion in the same manner. Thus, ion exchange mechanism would allow for a greater absorption of ions from the external medium than could normally be accounted for by free diffusion.



Diagrammatic representation of (a) The contact-exchange theory and (b) The carbonic acid exchange theory

Donnan equilibrium

The Donnan equilibrium theory takes into account the effect of fixed or in diffusible ions. Take, for example, a membrane that is permeable to some ions and not to others and which separates the cell from the external medium. Suppose in the inner side of this membrane there is a concentration of anions to which the membrane is impermeable (fixed anion). Now, if the above membrane is freely permeable to the cations and anions in the external solution equal numbers of cations and anions from the external solution will diffuse across from the membrane until an equilibrium is established. Normally, this equilibrium would also be electrically balanced. However, additional cations are needed to balance the negative charges of (fixed) anions. Therefore, the cation concentration would be greater in the internal solution than in external solution. also , it must be remembered , because , of the excess of negative charges due to fixed anions , the concentration of anions in the internal solution will be less than that of the external solution . As shown in figure 5.3.



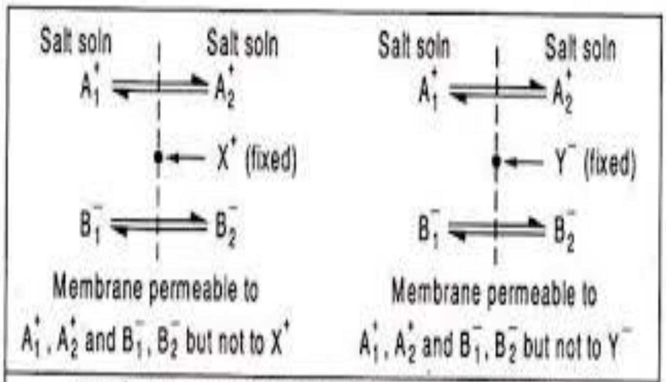


Fig. 5.3 : Diagrammatic representation of Donnan equilibrium

Donnan equilibrium ion diffiusion across membranes. (a) Membrane is impermeable to the cation, X^+ , causing additional anions , B^- , to diffuse across from the outside (accumulation of anions) . (b) membrane is the impermeable to the anion , Y^- , causing additional cations , A^+ , to diffuse across from the outside (accumulation of cations) .

Mass flow

Some of investigators believe that ions can move through roots along with the mass flow of water (**Hylmo, 1953; 1955; Kylin and Hylmo 1957**). According to this theory, an increase in transpiration should cause an increase in absorption of ions. That this is so has been generally accepted (**Russell, and barber, 1960**) but weather the effect of transpiration is direct or indirect is not clear. some authors claim that transpiration in directly effects ion absorption by removing ions after they have been released into the xylem ducts , causing by this dilution an increase in ion absorption activity (**Brauwer , 1956 ; Broyer et al . , 1943 ; Honert , 1955**) .

From this discussion, we have learned that at least part of the total salt taken up by a plant may result from passive absorption. This may be accomplished through free diffusion of ions into the apparent free space of a tissue. Accumulation of ions against a concentration gradient is possible under the above circumstances due to Donnan equilibrium. Accumulation may also take place against an apparent concentration gradient due to ion exchange mechanisms. Finally, the mass flow of ions through root tissue may be possible with the aid of transpirational ‘pull’. All of this mechanisms occur in the absence of metabolic energy. Let us now turn to an analysis of active transport.

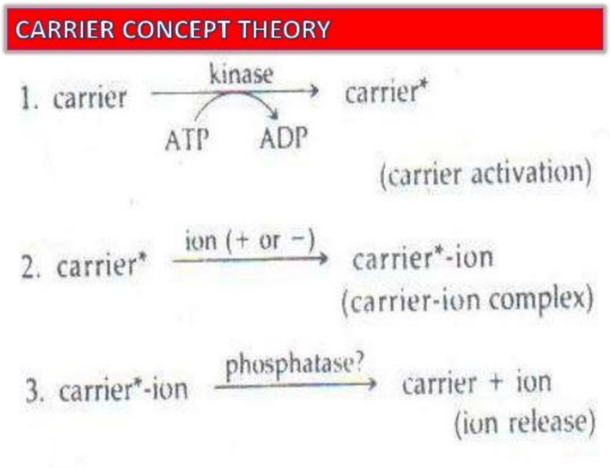
Active transport

Direct analyses of the vacuolar sap of plants immersed in solution of known salt concentration have demonstrated an equivocally that both anions and cations are accumulated by plants against concentration gradients. Furthermore, the extent of accumulation is such as known physical mechanisms, such as ion exchange and donnan equilibrium, cannot account for the extent of accumulation that occurs, analyses of the ion accumulation in the sap of *Nitella clavata* and *Valonia macrophysa* by **Hoagland (1944**) give an excellent picture both of the accumulation and selective properties of salt absorption mechanisms in plants.

Since ion accumulation is inhibited when the metabolic activity of the plant is inhibited by low temperature, low oxygen tension, metabolic inhibitors, etc., we can only assume that ion accumulation as it occurs in plants requires metabolic energy. The transport of ions with the aid of metabolic energy has been termed active transport. Various mechanisms have been devised to explain active transport, none of which have been universally accepted. All of this suggested mechanisms, however, generally accept the concept that the active transport of an ion across an impermeable membrane is accomplished through the mediation of a carrier compound present in the membrane.

The carrier concept

The space in a tissue or cell to which ions penetrate, through the mediation of metabolic energy, is termed inner space. Where outer space ends and inner space begins has not been clearly established. however , it is thought that this dividing line begins somewhere in the middle of the cytoplasm , since apparent free space volume measures have implied that part of cytoplasm allows for free diffusion of ions . The area between outer and inner space is impermeable to free ions. Passage across this area is thought to require the intercession of specific carriers, which combine with ions in outer space and release them in inner space. This impermeable barrier is usually spoken of as a membrane and the carriers as existing within it.



CARRIER CONCEPT THEORY

1. carrier $\xrightarrow[\text{ATP} \quad \text{ADP}]{\text{kinase}}$ carrier* (carrier activation)

2. carrier* $\xrightarrow{\text{ion } (+ \text{ or } -)}$ carrier*-ion (carrier-ion complex)

3. carrier*-ion $\xrightarrow{\text{phosphatase?}}$ carrier + ion (ion release)

The most important feature of the carrier theory is the assumption of an intermediate carrier-ion complex, which is capable of moving across the above mentioned impermeable membrane. The direction of movement of the complex is from outer to inner space only. Ions released into inner space cannot move out and thus are accumulated. A model giving a simplified description of the carrier concept is shown in figure 22.4.

The carrier concept has received impressive support by numerous investigators since its formulation by **Van den honert in 1937**. We will discuss three characteristics of salt absorption and active transport that appear to suggest strongly the validity of the carrier concept.

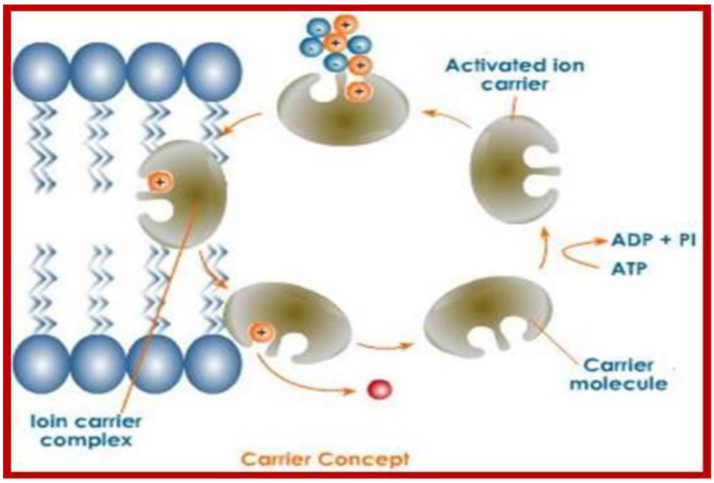


Fig. 22.4

<u>Saturation effects</u>

The fact that a level maximum rate of absorption may be maintained over a relatively long period of time suggests the participation of a finite number of carriers working, so to speak at maximum efficiency. That is, the active sites on the carriers in the above situation are occupied all of the time. As soon as a carrier released an ion to inner space, it is immediately occupied by an ion from the outer space areas in the tissue. Thus, at the saturation point of cycle is kept in continuous motion and cannot be made to proceed faster by increasing the salt concentration.

Specificity.

The carrier concept offers a reasonable explanation of the fact that roots selectively absorb ions. That is, ions are absorbed at different rates and have different levels in accumulation in the root tissue, suggesting the presence of specific carriers. This specificity is rather rigid with ions of dissimilar chemical behaviour, but weak or non-existent with ions of similar behaviour.

Cytochrome pump

Early workers observed that although salt accumulation is depended upon metabolic energy, there appeared to be no quantitative relationship between salty absorption and respiration. However, **lundeggardh and burstrom (1933)** claimed that such a relation exists between anion absorption and what they called ‘anion’ or ‘salt’ respiration. They observed that the rate of respiration increases when a plant is transferred from water to salt solution. The amount by which respiration is increased over normal or ground respiration by the transfer of a plant or tissue from water to a salt solution is known as salt respiration. The original observations of **lundegardh and Burstro** have since been expanded and developed to a workable theory in active salt absorption by **lundegardh (1950, 1954)**.

<u>Lundegardh theory assumes the following:</u>

1. Anion absorption is independent of cation absorption and occurs by a different mechanism.

2. An oxygen concentration gradient exists from the outer surface to the inner surface of a membrane, thus favouring oxidation at the outer surface and reduction at the inner surface

3. The actual transport of the anion occurs through a cytochrome system.

Since there is a quantitative correlation between anion absorption and salt respiration and since this correlation does not exist with cation absorption it was assumed that only anions are actively transported. The inhibition of salt respiration and consequent inhibition of anion absorption by cyanide or carbon monoxide led lundegardh to propose that transport of anions is mediated through cytochrome oxidase and that cytochromes may be anion carriers. A diagrammatic representation of lundegardh cytochrome theory is shown in figure 7.3. According to lundegardh theory, dehydrogenase reactions on the inner surface produce protons (H^+) and electrons (e^-). The electrons produced move outward via a cytochrome chain, while anions move inward. At the outer surface of the membrane the reduced iron of the cytochrome in oxidized, losing an electron and picking up an anion. The released electron unites with a proton and oxygen to form water.

At the inner surface the oxidized iron of the cytochrome becomes reduced by the addition of an electron released in a dehydrogenase reaction. The anion is released on the inside in this last reaction. Cations are absorbed passively to balance the potential difference caused by the accumulation of anions on the inner surface.

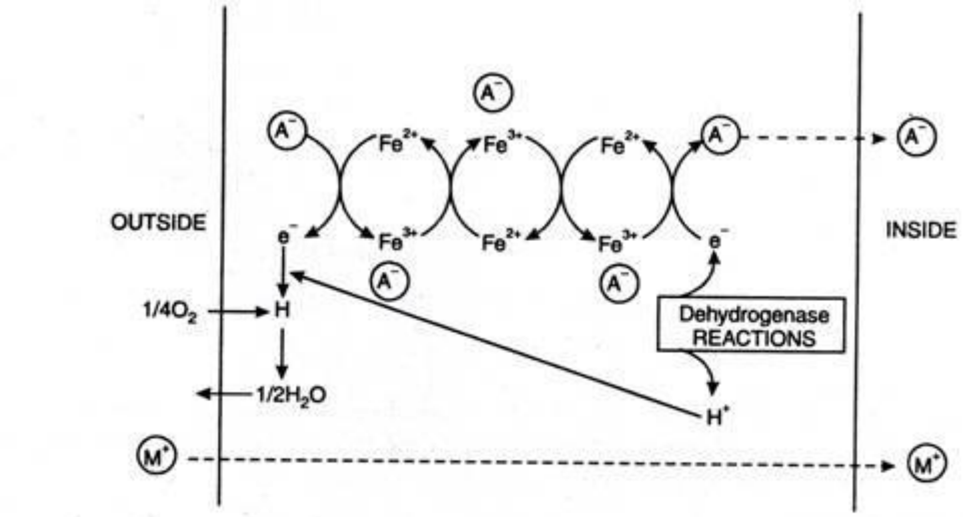


Fig. 7.3 Diagrammatic representation of the Lundegardh's cytochrome pump theory.

Although the cytochrome transport theory des give a clear picture of how metabolic energy might participate in ion absorption, it has not been universally accepted and has been criticized by a number of investigators. For example, **Robertson et al. (1951)** found that 2, 4- dinitrophenol (DNP), an inhibitor of oxidative

Phosphorylation, increases respiration but decreases salt absorption. This implies that phosphorylation should be included in any theory of ion accumulation. The original proposal that only anions are capable of stimulating respiration has come under considerable attack. For example, **Handley and overstreet (1955)** found that both potassium and sodium ions simulated respiration. Finally, if there is only one carrier for all anions, then competition for binding sites among anions should be apparent.

On the contrary, as pointed out in an earlier discussion, the anion sulfate, nitrate, and phosphate do not compete with one another.

Carrier mechanism involving ATP

A mechanism for active salt absorption that utilizes ATP has been proposed by **Bennet – clarck (1956).** This investigator has suggested that phospholipids may be important in the transport of ions across membranes otherwise impermeable. In this transport **lecithin**, a phospholipid, is synthesized and hydrolysed in a cyclic manner, picking up ions on the outer surface and releasing them on hydrolysis into inner space. The synthesis of at least one of the components of this phosphatide cycle requires ATP. A diagram showing the 'phosphatide cycle' and how it might proceed in ion transport is given in figure 7.4.

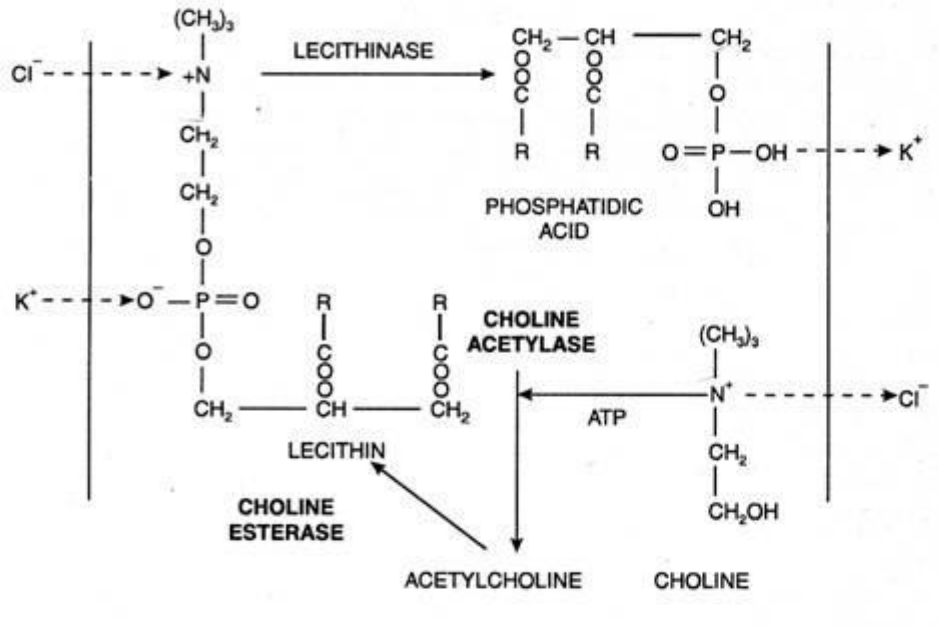


Fig. 7.4. Diagrammatic representation of the Bennet-Clark's Protein-Lecithin theory.

Factors affecting salt absorption

The physical and biochemical activities of living organisms are subject to the influences of their external and internal environments. Salt absorption is not an exception, being speeded up, slowed down, or kept in dynamic equilibrium by a complex of ever changing factors. The scientist has learned to study the influence of individual factors by controlling the environment and studying the effect of the one factor in question. This has been done with the process of salt absorption, and we now have an extensive, if incomplete, picture of how this process might proceed in nature's ever changing environment. We will discuss the effects of temperature, pH, light, oxygen tension, interaction, and growth on salt absorption.

Temperature

In general, an increase in temperature results in an acceleration of salt absorption.

However, the influence of temperature in salt absorption is confined to a relatively narrow range. In addition to accelerating salt absorption, increase in temperature past a maximum point will inhibit and eventually terminate the process. Most likely, the inhibitory effects of high temperature are because of the denaturation of enzymes involved either directly in salt absorption or in the synthesis of some necessary component of salt absorption.

Boss passive and active absorption process are affected by temperature changes. The rate of free diffusion, for example, depends upon the kinetic energy of the diffusing molecules or ion which is, in turn, dependent on temperature. Therefore, lowering of temperature will slow down any process dependent upon free diffusion. Low temperature will, of course, slow down the biochemical reactions found in active transport.

Hydrogen ion concentration

The availability of ions in the soil solution, discussed in a previous chapter, is profoundly affected by the hydrogen ion concentration. Ionization of electrolytes or the

Valence numbers of different ion species are influenced by changes in pH. For example, the monovalent phosphate ion, H_2PO^{4-} , is the form of phosphorus most readily taken up by plants. However, as a medium approaches a more alkaline pH, production of first the bivalent phosphate (HPO_4^{2-}) and then the trivalent phosphate (PO_4^{3-}) is favoured. The bivalent ion is only sparingly available to the plant, while the trivalent ion is not available at all. Since the monovalent ion is absorbed more readily than the bivalent ion, absorption of phosphate is accelerated at an acid pH. **Robertson (1958)** has pointed out that since boron is taken up as the undissociated acid, H_3BO_3, or as the $H2BO^{3-}$ ion, it too must be absorbed more readily at a lower pH. In contrast to the above observations, with anions increase in pH will favour the absorption of cations.

There have been numerous experiments showing little pH effect, as judged by growth (**Robertson, 1958**). Marked pH effects most likely occur when ion availability is inhibited. However, if the concentration of ion is high enough, it will be difficult to show a deficiency for that ion in the plant over a physiological range of pH values. Of course, at pH values outside the physiological range, damage to plant tissues and carriers will inhibit salt absorption.

Light

The effects of the light in the opening and closing of stomates and on photosynthesis indirectly affect salt uptake. Opened stomates increase the mass flow of water in the transpiration stream and thus may indirectly influence salt absorption. The energy derived from the photosynthetic process provides energy for salt uptake and the oxygen given off improves conditions for the active absorption of ions

Oxygen tension

The active phase of salt absorption is inhibited by the absence of oxygen. Indeed, it was this observation that most strongly supported early theories active transport.

Chapter 6

PLANT GROWTH REGULATORS

Plant growth regulators or phytohormones are organic substances produced naturally in higher plants, controlling growth or other physiological functions at a site remote from its place of production and active in minute amounts. **Thimmann (1948)** proposed the term *Phyto hormone* as these hormones are synthesized in plants. *Plant growth regulators* include auxins, gibberellins, cytokinins, abscisic acid and ethylene.

Plant growth regulators

An endogenous compound, which is synthesized at one site and transported to another site where it exerts a physiological effect in very low concentration. But ethylene (gaseous nature), exert a physiological effect only at a near a site where it is synthesized.

- Defined as organic compounds other than nutrients, that affects the physiological processes of growth and development in plants when applied in low concentrations.

- Defined as either natural or synthetic compounds that are applied directly to a target plant to alter its life processes or its structure to improve quality, increase yields, or facilitate harvesting.

Five major classes of plant hormones are known in plants. With progressing research, more active molecules are being found and new families of regulators are emerging.

(1) Auxin

(2) Gibberellin

(3) Cytokinin

(4) Abscisic acid

(5) Ethylene

Auxins

The term auxin is derived from the Greek word ‘auxein’ which means to grow. They are a class of plant hormones which has a cardinal role in coordination of many growth and behavioral processes in the plant's life cycle essential for development of plant. Auxin is the first plant hormone to be identified. They have the ability to induce cell elongation in stems and resemble indole acetic acid (the first auxin to be isolated) in physiological activity.

Discovery of auxin: **Darwin (1881)** was the first person who discovered the existence of auxin in plants, the first phytohormone known. He noted that the first leaf (coleoptile) of canary grass (Phalaris canariensis) was very sensitive and responsive to light and he demonstrated the bending of the grass coleoptiles towards unilateral source of light. This bending occurred only when the coleoptile was also illuminated. When the tip of the coleoptiles was covered with a black cap, it resulted in loss of sensitivity of the plant towards the light as shown in Figure 2. Darwin concluded that some influence that causes curvature is transmitted from the coleoptile tip to the rest of the shoot. Boysen – Jensen (1913) also made similar observations on oat (Avena) coleoptiles as shown in Figure 2. Paal (1918) demonstrated that when the decapitated coleoptiles tip was replaced on the cut end eccentrically, more growth resulted on the side which causes bending even when this is done in complete darkness.

Sites of biosynthesis of auxin: IAA is synthesized primarily in actively growing tissue in leaf primordia and young leaves, fruits, shoot apex and in developing seeds. It is made in the cytosol of cells.

Classification of auxins: Auxins are classified into two types based on its occurrence, if they occur naturally or are synthesized artificially.

1. Natural auxins
2. Synthetic auxins

Natural auxins: The four naturally occurring (endogenous) auxins are Indole-3-acetic acid, 4-chloroindole-3-acetic acid, phenylacetic acid and indole-3-butyric acid; only these four are synthesized by plants.

Synthetic auxins: Synthetic auxin analogs include 1-naphthaleneacetic acid, 2,4dichlorophenoxyacetic acid (2,4-D) and many others. Some synthetic auxins, such as 2,4D and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T), are used also as herbicides. Broad-leaf plants (dicots), such as dandelions, are much more susceptible to auxins than narrow-leaf plants (monocots) such as grasses and cereal crops, so these synthetic auxins are useful as synthetic herbicides.

Distribution of auxin in plants

In plants, auxin (IAA) is synthesized in growing tips or meristematic regions from where; it is transported to other plant parts. Hence, the highest concentration of IAA is found in growing shoot tips, young leaves and developing auxiliary shoots.

Within the plants, auxin may present in two forms. i.e., *free auxins* and *bound auxins*. Free auxins are those which are easily extracted by various organic solvents such as diethyl ether. Bound auxins on the other hand, need more drastic methods such as hydrolysis, autolysis, enzymolysis etc. for extraction of auxin. Bound auxins occur in plants as complexes with carbohydrates such as glucose, arabionse or sugar alcohols or proteins or amino acids such as aspartate, glutamate or with inositol.

Some physiological effects of auxin

1-Cell division and elongation

2- Apical dominance

3- Root initiation

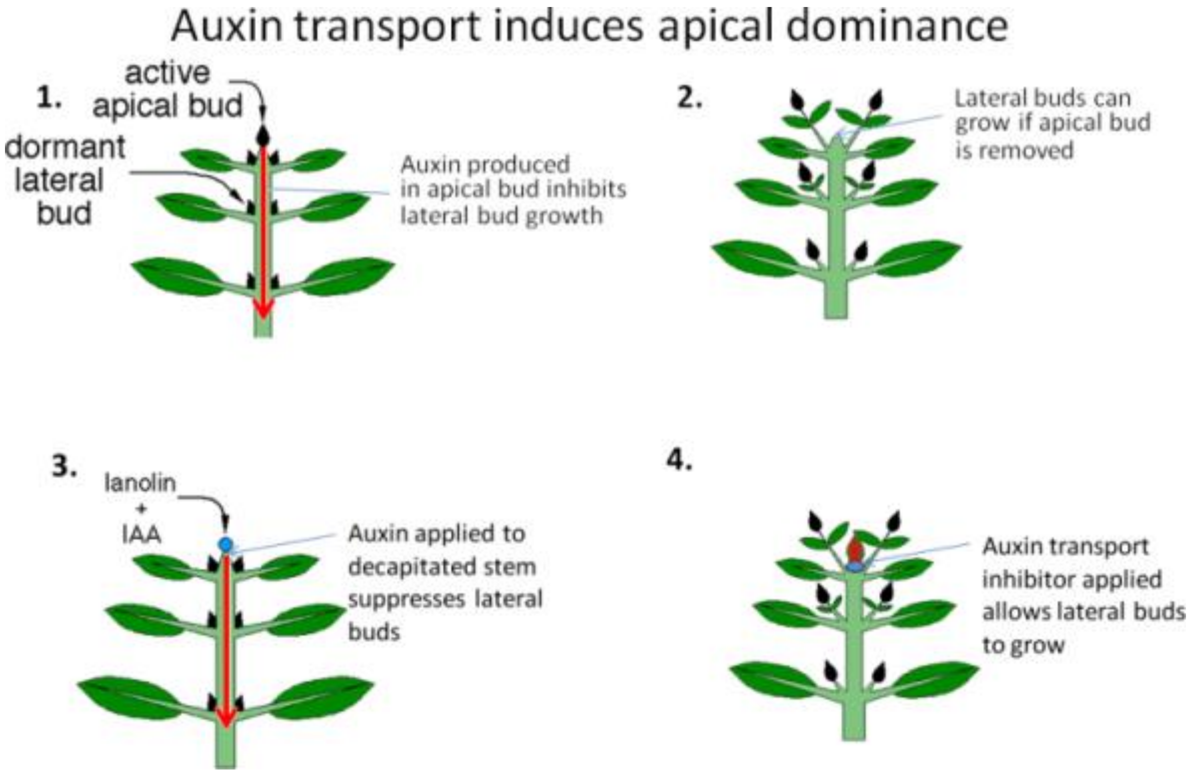
1. Cell division and elongation

The primary physiological effects of auxin are cell division and cell elongation in the shoots. It is important in the secondary growth of stem and differentiation of xylem and phloem tissues.

2. Apical dominance

In many plants, if the terminal bud is intact and growing, the growth of lateral buds just below it remains suppressed. Removal of the apical bud results in the rapid growth of lateral buds. This phenomenon in which the apical bud dominates over the lateral buds and does not allow the lateral buds to grow is known as *apical dominance*.

Skoog and Thimmann (1948) pointed out that the apical dominance might be under the control of auxin produced at the terminal bud and which is transported downward through the stem to the lateral buds and hinders the growth. They removed the apical bud and replaced it with *agar* block. This resulted in rapid growth of lateral buds. But when they replaced the apical bud with agar block containing auxin, the lateral buds remained suppressed and did not grow.

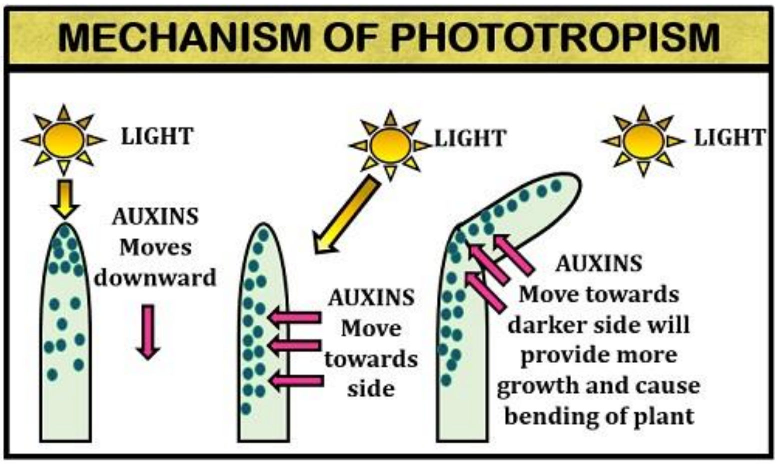


3. Root initiation

In contrast to stem, the higher concentration of auxin inhibits the elongation of roots but the number of lateral roots is considerably increased i.e., higher concentration of auxin induces more lateral branch roots. Application of IAA in lanolin paste to the cut end of a young stem results in an early and extensive rooting. This fact is of great practical importance and has been widely utilized to promote root formation in economically useful plants which are propagated by cuttings.

4. Phototropism

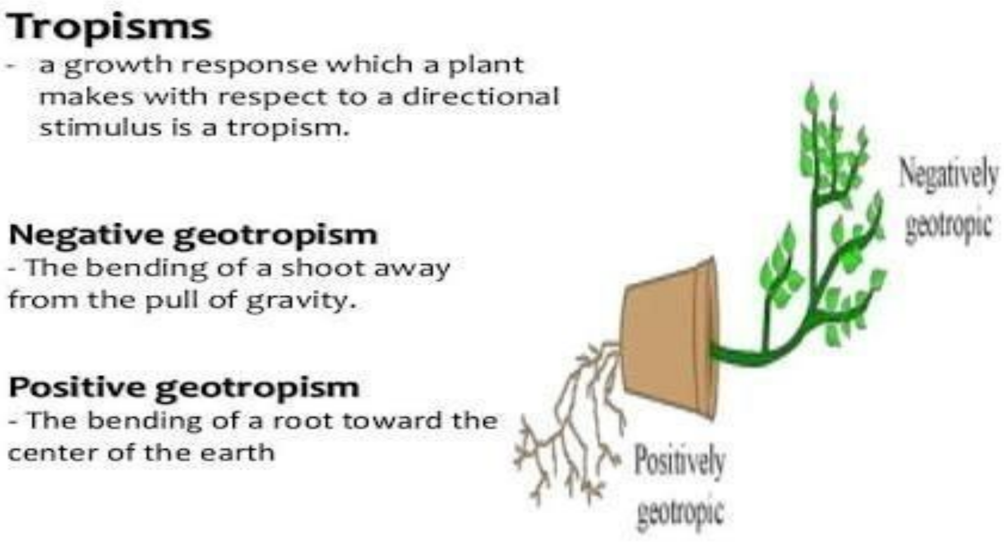
Photo means “**Light**” and tropism means “**Turning**”. Therefore phototropism merely refers as the bending of plants towards the light for its growth by absorbing solar energy.



When a growing plant is illuminated by unilateral light, it responds by bending toward the light. The bending of the plant is caused by cells elongating on the shaded side at a much greater rate than cells on the illuminated side. This differential of growth response of the plant to light, called phototropism, is caused by an unequal distribution of auxin, the higher concentration of the growth hormone being on the shaded side. Many attempts have been made to explain why there is a higher concentration of auxin on the shaded side of unilaterally illuminated coleoptile. There is a large evidence supporting the theory that unilateral illumination is capable of inducing lateral transport of auxin.

5. Geotropism

If an intact seedling is placed in a horizontal position it will respond to the earth's gravitational field with a particular pattern of growth. Growth of the stem under these circumstances will cause it to curve upward until it is vertical again and the root system will curve downward until it too is vertical again. Like phototropism, the geotropic response is controlled by an unequal distribution of auxin but, unlike phototropism, gravitational pull instead of light is the influencing factor in geotropic auxin distribution. The **colony-went** theory provides an explanation for geotropism as well as phototropism. They proposed that the differential growth exhibited by a horizontally placed organ is due to the accumulation of auxin on the lower side. They suggested that auxin is laterally transported from the upper to the lower side under the influence of gravity. The accumulation of auxin on the lower side of a horizontally placed stem causes an accelerated growth to occur on the lower side causing the stem to curve upward. The horizontally placed root, however, will exhibit a positive geotropic response even though auxin concentrates on the lower side. Roots are much more sensitive to IAA than stems and the concentrations of IAA which stimulate cell elongation in stems are actually inhibitory to cell elongation in roots. The accumulation of auxin on the lower side of a horizontally placed root would, therefore, retard cell elongation on that side.



Tropisms

- a growth response which a plant makes with respect to a directional stimulus is a tropism.

Negative geotropism

- The bending of a shoot away from the pull of gravity.

Positive geotropism

- The bending of a root toward the center of the earth

Gibberellin

Gibberellin was first discovered in Japan by **Kurusowa**. He observed from his field that some of the rice seedlings had grown much taller than the others. On further observation, he found that such taller rice plants had shown unusual internodal elongation. This internodal elongation is known as the ‘bakanae’ or ‘foolish seedling’ disease of rice. Later, it was discovered that the elongation was due to the action of a substance produced by a fungus, Gibberella fujikuroi. This substance was successfully isolated from the fungus and it was named as gibberellic acid.

There are over 90 different gibberellins isolated from fungi and from higher plants. Gibberellins occur in various plant organs.

They are named as GA1, GA2, GA3, etc. These phytohormones occur in all groups of plants.

Physiological effects of gibberellin

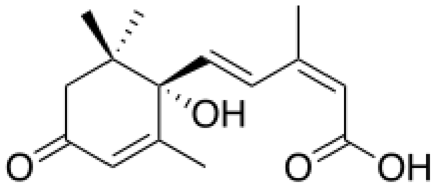
1. Gibberellins produce extraordinary elongation of stem. The elongation of stem is caused by the cell division and cell elongation induced by gibberellic acid.
2. One of the most striking effects of the gibberellins is the reversal of dwarfism in many genetically dwarf plants. For e.g. ‘Rosette’ plant of sugar beet, when treated with GA undergoes marked longitudinal growth of axis attaining the normal size.
3. Rosette plants usually show reduced internodal growth. These plants exhibit excessive internodal growth when they are treated with gibberellin. This sudden elongation of stem followed by flowering is called bolting.
4. Many biennials usually flower during the second year of their growth. For flowering to take place, these plants should be exposed to cold season. Such plants could be made to flower without exposure to cold season in the first year itself, when they are treated with gibberellins.

5. Formation of seedless fruits without fertilization can also be induced by gibberellin treatment in many plants. e.g. Tomatoes, apples, cucumbers, etc.,
6. Some of the light sensitive seeds can germinate by the treatment of gibberellic acid even in complete darkness. e.g. barley, gibberellin breaks dormancy in potato tubers.

Cytokinins

The effect of cytokinins was first reported when it was found that adding the liquid endosperm of coconuts to developing plant embryos in culture stimulated their growth. The stimulating growth factor was found to be cytokinin, a hormone that promotes cytokinesis (cell division). Almost 200 naturally-occurring or synthetic cytokinins are known, to date. Cytokinins are most abundant in growing tissues, such as roots, embryos, and fruits, where cell division is occurring. Cytokinins are known to delay senescence in leaf tissues, promote mitosis, and stimulate differentiation of the meristem in shoots and roots. Many effects on plant development are under the influence of cytokinins, either in conjunction with auxin or another hormone. For example, apical dominance seems to result from a balance between auxins that inhibit lateral buds and cytokinins that promote bushier growth.

Abscisic acid



Abscisic acid

Abscisic acid (also called ABA) is one of the most important plant growth inhibitor. It was discovered and researched under two different names before its chemical properties were fully known, it was called *dormin* and *abscicin II*. Once it was determined that the two compounds are the same, it was named abscisic acid. The name "abscisic acid" was given because it was found in high concentrations in newly abscissed or freshly fallen leaves.

This class of PGR is composed of one chemical compound normally produced in the leaves of plants, originating from chlorplasts, especially when plants are under stress. In general, it acts as an inhibitory chemical compound that affects bud growth, and seed and bud dormancy. It mediates changes within the apical meristem, causing bud dormancy and the alteration of the last set of leaves into protective bud covers. Since it was found in freshly abscissed leaves, it was thought to play a role in the processes of natural leaf drop, but further research has disproven this. In plant species from temperate parts of the world, it plays a role in leaf and seed dormancy by inhibiting growth, but, as it is dissipated from seeds or buds, growth begins. In other plants, as ABA levels decrease, growth then commences as gibberellin levels increase. Without ABA, buds and seeds would start to grow during warm periods in winter and be killed when it froze again. Since ABA dissipates slowly from the tissues and its effects take time to be offset by other plant hormones, there is a delay in physiological pathways that provide some protection from premature growth. It accumulates within seeds during fruit maturation, preventing seed germination within the fruit, or seed germination before winter. Abscisic acid's effects are degraded within plant tissues during cold temperatures or by its removal by water washing in out of the tissues, releasing the seeds and buds from dormancy.

In plants under water stress, ABA plays a role in closing the stomata. Soon after plants are water-stressed and the roots are deficient in water, a signal moves up to the leaves, causing the formation of ABA precursors there, which then move to the roots. The roots then release ABA, which is translocated to the foliage through the vascular system and modulates the potassium and sodium uptake within the guard cell, which then lose turgidity, closing the stomata. ABA exists in all parts of the plant and its concentration within any tissue seems to mediate its effects and function as a hormone; its degradation, or more properly catabolism, within the plant affects metabolic reactions and cellular growth and production of other hormones. Plants start life as a seed with high ABA levels. Just before the seed germinates, ABA levels decrease; during germination and early growth of the seedling, ABA levels decrease even more. As plants begin to produce shoots with fully functional leaves, ABA levels begin to increase, slowing down cellular growth in more "mature" areas of the plant. Stress from water or predation affects ABA production and catabolism rates, mediating another cascade of effects that trigger specific responses from targeted cells. Scientists are still piecing together the complex interactions and effects of this and other phytohormones.

Ethylene

Ethylene is a gas that forms through the breakdown of methionine, which is in all cells. Ethylene has very limited solubility in water and does not accumulate within the cell but diffuses out of the cell and escapes out of the plant. Its effectiveness as a plant hormone is dependent on its rate of production versus its rate of escaping into the atmosphere. Ethylene is produced at a faster rate in rapidly growing and dividing cells, especially in darkness. New growth and newly germinated seedlings produce more ethylene than can escape the plant, which leads to elevated amounts of ethylene, inhibiting leaf expansion. As the new shoot is exposed to light, reactions by phytochrome in the plant's cells produce a signal for ethylene production to decrease, allowing leaf expansion. Ethylene affects cell growth and cell shape; when a growing shoot hits an obstacle while underground, ethylene production greatly increases, preventing cell elongation and causing the stem to swell. The resulting thicker stem can exert more pressure against the object impeding its path to the surface. If the shoot does not reach the surface and the ethylene stimulus becomes prolonged, it affects the stem's natural geotropic response, which is to grow upright, allowing it to grow around an object. Studies seem to indicate that ethylene affects stem diameter and height: When stems of trees are subjected to wind, causing lateral stress, greater ethylene production occurs, resulting in thicker, more sturdy tree trunks and branches. Ethylene affects fruit-ripening: Normally, when the seeds are mature, ethylene production increases and builds-up within the fruit, resulting in a climacteric event just before seed dispersal. The nuclear protein Ethylene

Insensitive2 (EIN2) is regulated by ethylene production, and, in turn, regulates other hormones including ABA and stress hormones.

Seed dormancy

Plant hormones affect seed germination and dormancy by acting on different parts of the seed.

Embryo dormancy is characterized by a high ABA: GA ratio, whereas the seed has a high ABA sensitivity and low GA sensitivity. In order to release the seed from this type of dormancy and initiate seed germination, an alteration in hormone biosynthesis and degradation toward a low ABA/GA ratio, along with a decrease in ABA sensitivity and an increase in GA sensitivity, must occur.

ABA controls embryo dormancy, and GA embryo germination. Seed coat dormancy involves the mechanical restriction of the seed coat. This, along with a low embryo growth potential, effectively produces seed dormancy. GA releases this dormancy by increasing the embryo growth potential, and/or weakening the seed coat so the radical of the seedling can break through the seed coat. Different types of seed coats can be made up of living or dead cells, and both types can be influenced by hormones; those composed of living cells are acted upon after seed formation, whereas the seed coats composed of dead cells can be influenced by hormones during the formation of the seed coat. ABA affects seed coat growth characteristics, including thickness, and effects the GA-mediated embryo growth potential. These conditions and effects occur during the formation of the seed, often in response to environmental conditions. Hormones also mediate endosperm dormancy: Endosperm in most seeds is composed of living tissue that can actively respond to hormones generated by the embryo. The endosperm often acts as a barrier to seed germination, playing a part in seed coat dormancy or in the germination process. Living cells respond to and also affect the ABA:GA ratio, and mediate cellular sensitivity; GA thus increases the embryo growth potential and can promote endosperm weakening. GA also affects both ABA-independent and ABA-inhibiting processes within the endosperm.

References

Else MA, Coupland D, Dutton L, Jackson MB ***(January 2001).*** *"Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure, and slows leaf expansion in flooded plants of castor oil (Ricinus communis) despite diminished delivery of ABA from the roots to shoots in xylem sap". Physiologia Plantarum.* ***111*** *(1): 46–54. doi:10.1034/j.1399-3054.2001.1110107.x.*

Feurtado JA, Ambrose SJ, Cutler AJ, Ross AR, Abrams SR, Kermode AR (February 2004). *"Dormancy termination of western white pine (Pinus monticola Dougl. Ex D. Don) seeds is associated with changes in abscisic acid metabolism". Planta.* ***218*** *(4): 630–9. doi:10.1007/s00425-003-1139-8. PMID 14663585.*

Gerhard W (2000). "Seed Dormancy". *The Seed Biology Place*. Royal Holloway University of London.

Kermode AR (December 2005). *"Role of Abscisic Acid in Seed Dormancy". J Plant Growth Regul.* ***24*** *(4): 319–344. doi:10.1007/s00344-005-0110-2.*

Ren H, Gao Z, Chen L, Wei K, Liu J, Fan Y, Davies WJ, Jia W, Zhang J (2007). *"Dynamic analysis of ABA accumulation in relation to the rate of ABA catabolism in maize tissues under water deficit". Journal of Experimental Botany.* ***58*** *(2): 211–9. doi:10.1093/jxb/erl117. PMID 16982652. Archived from the original on 2012-07-10.*

Robert M. Devlin (1969)**:** plant physiology, university of Massachusetts. Second edition. Mineral nutrition part.

Wang Y, Liu C, Li K, Sun F, Hu H, Li X, et al. (August 2007). "Arabidopsis EIN2 modulates stress response through abscisic acid response pathway". *Plant Molecular Biology*. **64** (6): 633–44. doi:10.1007/s11103-007-9182-7. PMID 17533512.

Yan J, Tsuichihara N, Etoh T, Iwai S (October 2007). *"Reactive oxygen species and nitric oxide are involved in ABA inhibition of stomatal opening". Plant, Cell & Environment.* ***30*** *(10): 1320–5. doi:10.1111/j.1365-3040.2007.01711.xPMID 17727421.*