UNIT 2

MERISTEMATIC TISSUES

Structure

2.1 INTRODUCTION

In the last unit you have studied the different type of simple and complex tissues found in the plants. Higher plants possess small, organized regions of active cell division, cell enlargement, differentiation termed as meristems. The growth and morphogenesis of the plant is controlled by these meristematic regions. The meristematic regions located on the tip of the stem and root is referred as apical meristems. Some meristematic regions are found in the lateral regions and some at regions such as internodes, regions where the leaves attach and leaf bases. These are referred to as lateral and as intercalary meristems. In the present unit we will describe various types of meristematic tissues present in the plants along with their functions. We will also discuss about theories proposed related to organization of root and shoot apex.

Objectives

After studying this unit you would be able to :

- describe various types of meristems;
- discuss the role of various meristems in plants;
- describe various components of root and shoot apical meristem; and
- explain various theories related to root apical organisation and shoot apical organisation.

2.2 APICAL MERISTEMS

As you know that apical meristem are located terminally in plants. These are found at the apices or growing points/tips of root and shoot (Fig.2.1). They first appear in embryonic root and shoot. All the primary tissues originate from this meristem. Cell divisions and subsequent cell enlargement in these areas lengthen the above and below ground parts of the plant. They help in the growth of the root as well as shoot. Depending upon their position in the plant they have been categorized as shoot apical and root apical meristem.

Shoot apical meristem- It is located at the terminal position of the shoot. It is a dome shaped structure or nearly flattened reservoir of embryonic cells present at the terminal end of the shoot/stem. The cells in the region divide continuously to form new tissues and organs. The cells in the region possess the capacity for unlimited growth. This part lies (distal to the youngest) immediately above the leaf primordium. It is variable in shape at different stages of plant development. It is usually radially symmetrical and appears to be more or less convex in a median longitudinal section. The shoot apex shows rhythmic changes before and after the initiation of leaf primordium. It widens before initiation of leaf and again becomes narrow.

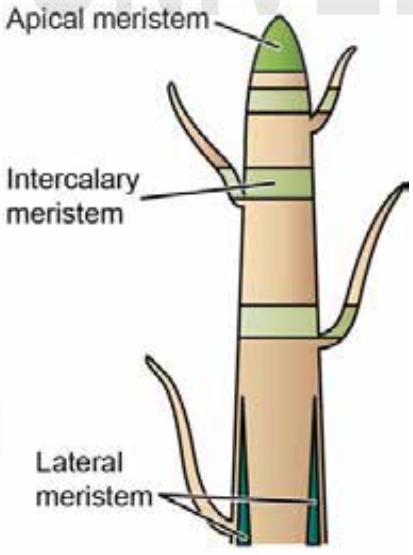

Fig. 2.1: Position of various meristems in the plant.

The shoot apical meristem is the source of initiation of all the above ground organs. Cells of the shoot apical meristem serve as stem cells and proliferate and get incorporated into differentiating leaf or flower primordia. In fact, the

primordial of leaves, sepals, petals, stamens and ovaries are initiated at the shoot apical meristem at the rate of one every time interval. This time interval is called a **plastochron**. New leaves are produced at regular time intervals if temperature is held constant. Thus by using indices of leaf plastochron, age of a plant can be determined on the basis of its morphological traits rather than on chronological age. It is of advantage as one can eliminate some differences caused by germination, developmental differences and exponential growth.

Root apical meristem- The meristematic cells located at the apex of the root comprises the root apex meristem. This region differentiates into embryonic radicle. The cells of this region are densely cytoplasmic with large nuclei.

2.3 LATERAL MERISTEMS

These meristem are lateral in position lie paralled to the long shoot and root axes (Fig. 2.1). These meristems help in increasing the thickness of the plants. The cells are arranged parallel and normally divide periclinally or radially and give rise to secondary permanent tissues. The vascular cambium and the cork cambium are good examples of lateral meristems. You will study about lateral meristem in Unit 6 of this course.

Vascular cambium- Some plants grow in diameter by producing new tissues laterally from a cylinder of tissue called the vascular cambium**.** This tissue extends throughout the length of the plant from the tips of the shoots to the tips of the roots. It is present in all perennial and some annual plants. The cells of vascular cambium produce secondary tissues after division.

Cork cambium is also referred as **phellogen.** They are found in the bark of roots and stems of woody plants where they produce cork cells. The cork cambia originate just under the epidermis of the primary body. In some trees they are produced as long cylinders running parallel to the vascular cambium.

2.4 INTERCALARY MERISTEM

It lies between the region of permanent tissues and is considered as a part of primary meristem which has become detached due to formation of intermediate permanent tissues. It is found either at the base of leaf or at the base of internodes. In *Pinus* it is located at the base of leaf but in grasses it is located at the base of internode. The intercalary meristems help in increasing the length of the internode. Grasses have intercalary meristems located along the stems near the nodes. Cell divisions in this tissue push the stem upward. Monocots do not possess lateral meristems. Hence in these plants, the lateral increase in size is the result of primary tissue cell enlargement but not cell division.

SAQ 1

Differentiate between the following:

a) Root and Shoot apical meristem.

b) Vascular and Cork cambium.

c) Apical, Lateral and Intercalary meristems.

2.5 THEORIES OF ROOT APICAL ORGANISATION

All the cells in a given primary root owe their origin to these cells which constitute the so called root apical meristem. The cell(s) present in the meristem are termed as initial(s). Since they are localized in root apices, they are referred to as root-apical initials. Though, all roots are characterized by the presence of such initials, yet their number, location, placement and mode of function are not fully understood. All plant species do not necessarily possess exactly similar root apical structure. A large diversity is recorded in this context. Many attempts have been made in the past to provide an insight into the organisation of root apex.

The meristem of the primary root gets differentiated in the embryonic radical. The cells present in the root apical region are densely cytoplasmic with large nuclei. They are undifferentiated and undergo active division. The mature tissues of the root are derived from these cells or initials. The root apex at the tip is enclosed within the structure called root cap. The apical meristem in root is subterminal in position. This meristem is not associated with the formation of lateral appendages. The meristem does not undergo any rhythmic changes in shape and size of the root apex. The root cap occupies the terminal position (Fig. 2.2). The three tissue systems namely epidermis, cortex and vascular cylinder are located behind the root apex.

Different theories have been proposed by several workers to depict the structure and functional organisation of the root apical meristem. We will now discuss a few of such works.

2.5.1 Apical Cell Theory

In roots of certain vascular cryptogams (Example- *Equisetum, Ophioglossum, Dryopteris)* only a single tetrahedral apical cell is present (Fig. 2.3 a), It is suggested that all the cells in a root are derived from it. This forms the basis of **apical cell theory**. Apical cell theory was proposed by **Hofmeister** (1852) and supported by **Nageli** (1859). A single apical cell is the structural and functional unit. According to this theory a single tetrahedral shaped apical cell has been noted in number of vascular cryptograms. The divisions in the apical cell give rise to tissues of the root. The upper portion of the apical cell gives rise to the tissues forming the body of the root while the lower or the basal side of the apical cell forms the root cap. This concept was not accepted because unlike the presence of a single cell initial in cryptogams, there are infact, a group of apical cells in flowering plants.

2.5.2 Histogen Theory

This theory was proposed by **Hanstein** in 1868. He postulated the existence of three cell-initiating centres or regions which he termed as **histogens**. He suggests the existence of layers of meristems or histogens in the root apex. These include **dermatogen**, **periblem** and **plerome**. Each layer has a specific function. The dermatogen gives rise to epidermis, periblem gives rise to cortex while plerome forms the vascular cylinder of the mature root (Fig. 2.2). Later on **calyptrogen** was designated as the fourth histogen. This histogen played a role in formation of root cap. Later on Haberlandt in 1914 proposed the names **protoderm**, **ground meristem** and **procambium** for dermatogen, periblem and plerome respectively.

Several other workers also described the root apex in terms of layer of initial cells or histogens. **Schüepp** in 1926 divided the root apical meristem into different zones on the basis of cellular configuration. These include **type A** - all tissues of the root apex including root cap are derived from a single apical cell as noted in vascular cryptograms; **type B** - there are two group of initials. One that give rise to vascular cylinder and the other group forms the cortex, epidermis and root cap. In **type C** - poorly organized initials give rise to vascular cylinder, cortex and root cap, and **type D**- three groups of initials give rise to vascular cylinder, cortex, epidermis and root cap respectively.

Guttenberg (1960) proposed that in the root apex, the meristems of different tissue systems are placed at varying distance from the central initial cells. According to him the root apices are of two types- i) **closed type**- in this type the initials of tissues are discrete and lie immediately adjacent to the central cells. Separate initials give rise to vascular cylinder and cortex, while root cap or protoderm may have common or separate initials; ii) **open type**- in this type of meristem, different tissues are at distance from the central cells. Common initials are found for tissue systems except vascular cylinder. Thus in this system, the earlier described types C and D show closed type organization while A and B show open type of organisation.

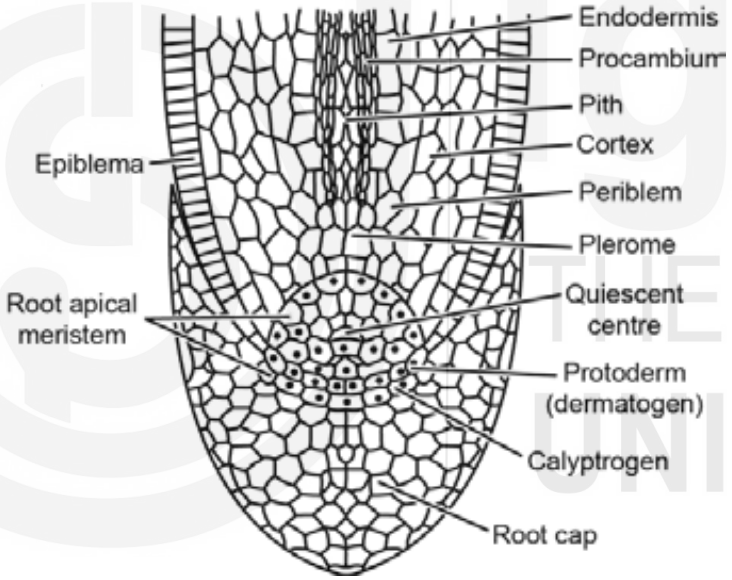

Fig. 2.2: Diagrammatic representation of the root apex.

2.5.3 Korper-Kappe Theory

This theory was proposed by **Schüepp** in 1917. He explained the organization of root apex in terms of planes of division. According to him, the cells of the root apex divide in two planes. First cell divides into two by transverse division and then one of the daughter cell divides by longitudinal division. The sequence of division is termed as 'T' division. On the basis of these divisions, two zones Korper and Kappe were differentiated in the root system. In some parts of the root i.e. outer region, the 'T' is straight. After the first horizontal division the daughter cells divide longitudinally. In the inner region, 'T' is inverted (Fig. 2.3 b). The second division takes place in the upper daughter cell. the zone with inverted 'T' type divisions are termed as **Korper** (cap) and those taking place in straight 'T' are termed as **Kappe** (body). In monocotyledons a sharp boundaries between Korper and Kappe has been noted (Fig. 2.3 c).

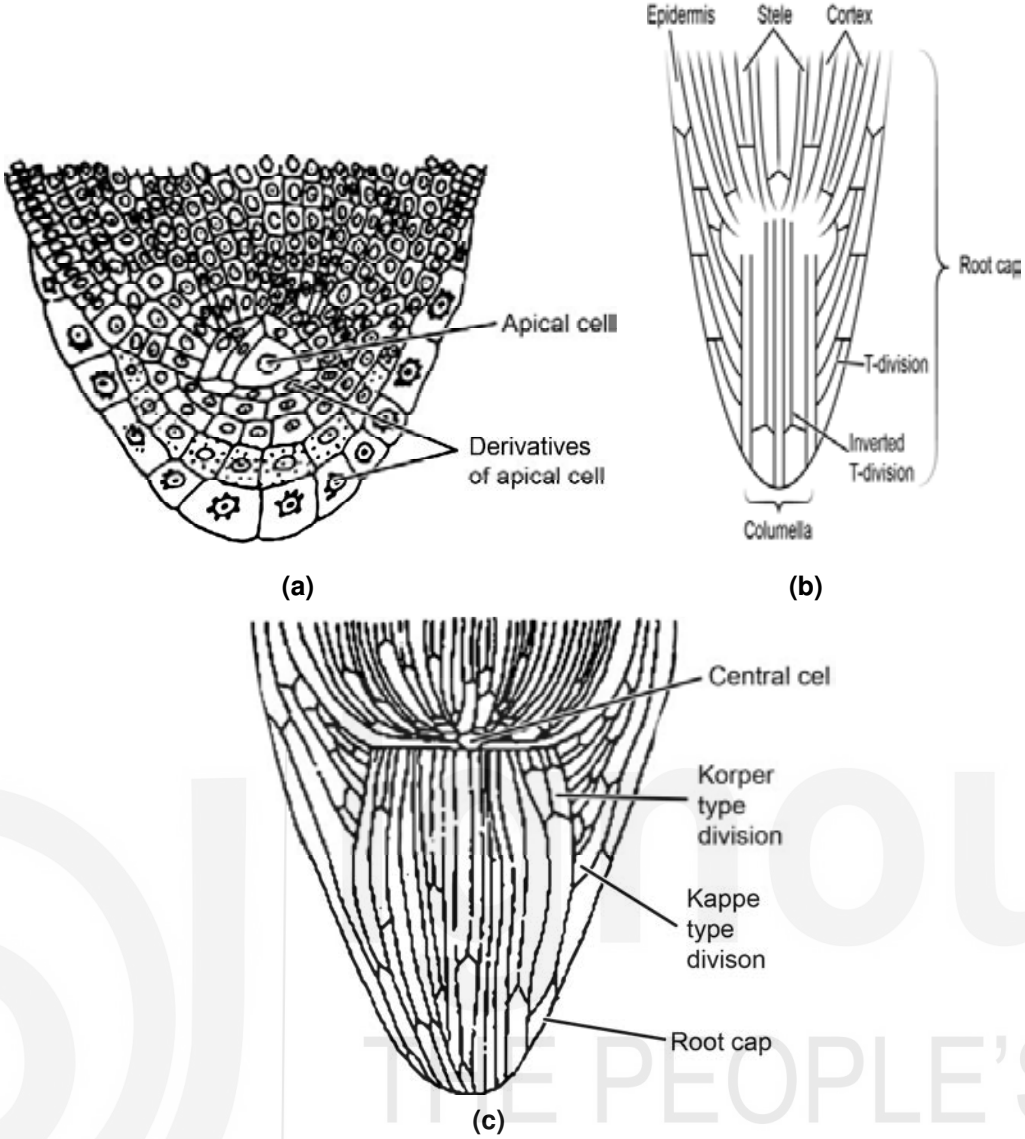

Fig. 2.3: Representation of root apical meristems a) Median longitudinal section of the root tip of *Pteris,* showing single apical cell with four cutting faces (one not in plane of section). (Modified from A. J. Eames and L.H. McDaniels , A*n Introduction to Plant Anatomy* McGraw - Hill Book Co., Inc., New York); b) T division noted in the root cells; c) Root apex of *Zea mays* in longitudinal section showing pattern of cell lineages, interpreting its organization on Korper-Kappe concept. (Adopted from F.A.L. Clowes, Endeavour, 24, 1965).

2.5.4 Function of Root Cap and Quiescent Center

Root cap

The tip of the root is covered by the group of parenchymatous cells that form the root cap. Root cap occupies terminal position of the root (Fig. 2.4). It protects the meristem and function in regulation of growth, production and secretion of mucilage. The peripheral cells of the root cap secrete mucilage called mucigel thus making outer walls of the root cap are mucilaginous and help to reduce friction between apex of the root and hard soil during root penetration in the soil. It also helps in absorption of water and nutrients.

The root cap originates by the activity of root meristem and consists of centrally positioned longitudinally aligned columella cells and outer peripheral cells. With growth of the root, the root cap cells are pushed through the cap

and eventually sloughed off in great numbers by friction. The columella cells are elongated having dense aggregation of starchy amyloplast that sediment to lower side in response to gravity.

In dicotyledons it arises from same initials which form epidermis while in monocotyledons it arises from separate set of initials. The cells of the root cap become more differentiated as the distance from the root tip increases. If the root cap is removed the cells of the quiescent center divide rapidly to form new root cap.

In open meristem the founder cells in the distal part of the **quiescent center** contribute initials and progeny to the root cap. In closed system, the thick polylamellate wall may accrete (growth or increase by the gradual accumulation of additional layers or matter) between the root and root cap. The root cap does not possess reservoir of cells that replace and rejuvenate its set of initials. Lack of reservoir of cells leads to end of mitosis, endopolyploidy and senescence of the cap followed by damage to the primary root tip. The roots are replaced by secondary roots and fibrous root system gets developed. Monocots generally possess fibrous root system. Woody plants are example of open meristems and distinct caps.

Mitotically active cells of the root apical meristem present in the proximity of the root cap form the region of cell division. Behind this point there is a zone where the cells divide less actively but the rate of expansion or extension increases. The region is referred as the **region of cell elongation** or **radial enlargement** (Fig. 2.4). Another region of maturation comprising of longitudinal cells depicting capacity of tissue differentiation is also evident near the apical meristem. The younger less differentiated cells are present near the root apex while the larger, mature cells are located at distances from the apex. Some workers have shown T divisions in the meristematic cells. The cells divide transversely followed by longitudinal division in one of the daughter cells. Two cells formed by longitudinal division form the progenitor of the longitudinal rows into the root axis and root cap. The upper daughter cells divide longitudinally to form an inverted T. In the cells giving rise to the root cap, the lower daughter cells divide longitudinally to form an upright T.

Quiescent center

Clowes (1956) discovered a central cup like region of cells lying between the root cap and the active meristematic region. **Quiescent center** is referred to hemispherical shaped aggregation of mitotically and metabolically inactive cells positioned just behind the root cap. This is also referred as inactive region of the root (Fig. 2.4). The cells in the zone divide 10 to 20 times slower than the adjacent cells. They do not participate in the formation of mature root tissues. The cells present in this region possess low concentration of DNA, RNA and protein. The cells have less mitochondria, endoplasmic reticulum and dictyosomes. The cells of this region do not synthesize DNA but in some cases may show a slow rate of DNA synthesis and cell cycle. The cells remain arrested in the G1 phase of the mitosis.

This region has been recognized in root tip of large number of plants. It is generally hemispherical in shape and contains several hundred cells.

According to Clowes (1959), the cells of the quiescent center are inactive because of their localization in the apical meristem. The antagonistic direction of cell growth in various parts of the meristem or the presence of rapidly dividing cells around the region could be responsible for the inactivation of the cells of quiescent center. The cells of the quiescent center become active whenever the previous initials are damaged. Thus the center acts as the reservoir of cells resistant to the damage because of their inactive nature. They act as the source of active initials. It has been proposed that when the root cells are exposed to toxic doses of X rays, the meristematic cells stop synthesizing DNA but the cells of the quiescent center become active and synthesize DNA. This is because cells of the quiescent center are resistant to irradiations in comparison to the actively dividing cells.

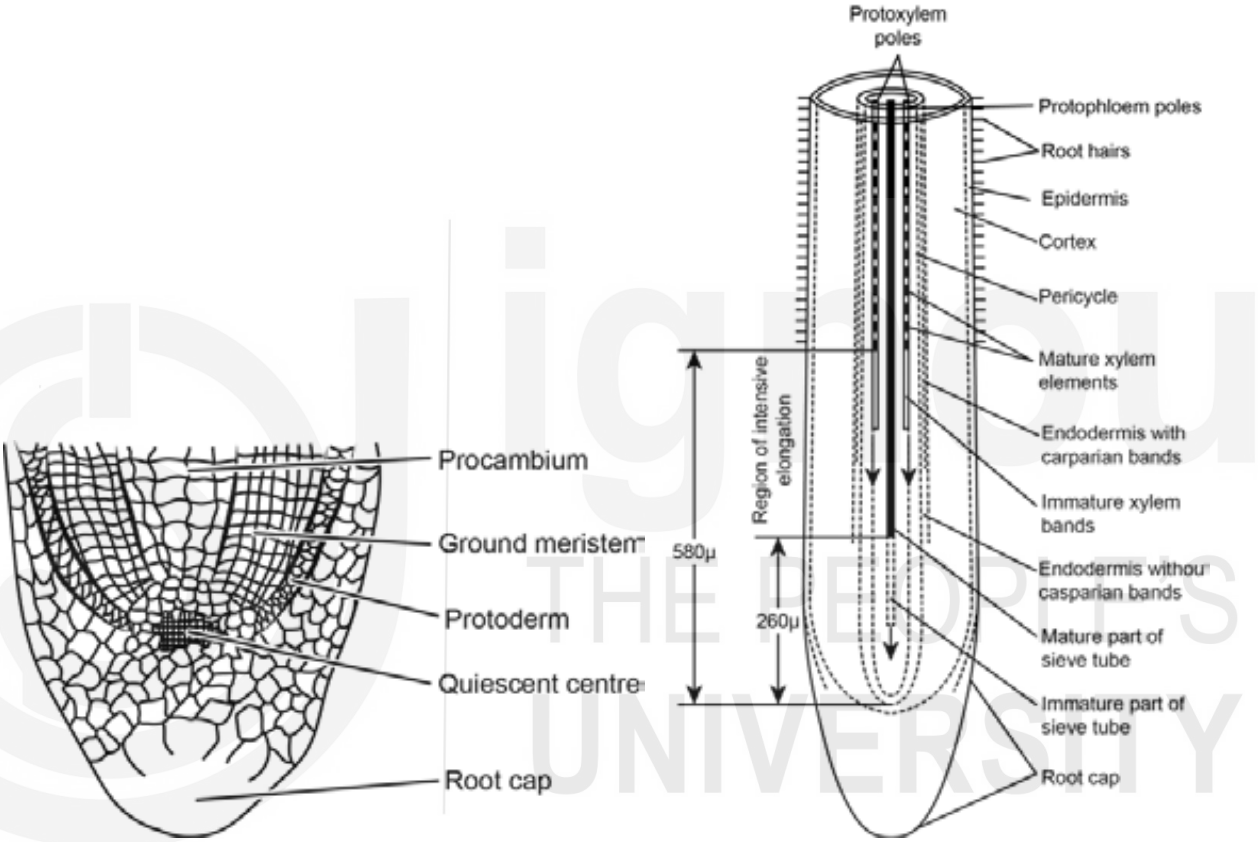

Fig. 2.4: Portion of the root cap showing quiescent center.

SAQ 2

a) Answer in one word

i) It is located at the terminal position of the shoot.

ii) These meristems help in increasing the thickness of the plants. The cells are arranged parallel and normally divide periclinally to give rise to secondary permanent tissues.

iii) In roots of certain vascular plants a single tetrahedral apical cell is present which give rise to root tissues.

iv) Apical cell theory was proposed by him.

v) In 1868 Hanstein proposed this theory.

vi) According to this theory T divisions in the root zone take place.

b) Write in brief the function of :

i) Root cap

ii) Quienscent center

iii) Vascular cambium

2.6 THEORIES OF SHOOT APICAL ORGANIZATION

This meristem occupies terminal position in the shoot i.e. they are located at the apex of shoot. The primary new tissues and plant organs originate from them. It is self determining and autonomous center of the plant. This part lies immediately above the leaf primordia. It is variable in shape and size at different stages of plant development. The shoot apex meristem undergoes rhythmic changes in shape and size before the initiation of leaf primordium. It widens before leaf initiation but becomes narrow after leaf initiation.

The shoot apical meristems are simple structure in vascular cryptogams. The apical cell is pyramidal in shape with three or four faces pointing downward and one face pointing upward forming outer part of the plant. The apical cell divides in an orderly manner (asymmetric division) and produces narrow flat cells. The next division is also asymmetric and small thin walled daughter cells are produced. The process is repeated several times and the packet of cells develop into segments of the shoot.

In seed plants the shoot apical meristem does not show any distinctive cell as in cryptograms. The apical meristem is supposed to be composed of two zones- outer **tunica** and inner **corpus**. They are distinguished from each other on the basis of plane of division. The cells of tunica region divide only with anticlinal walls, walls perpendicular to the surface of tunica. The tunica layer grows as a sheet. When tunica is single layered it is referred as **monostratose** but when it is two or more layered it is called as **multistratose**. The corpus is covered over by tunica. The corpus consists of cells which divide in any direction, hence the region can grow in three dimensions. In monocots the periclinal divisions are common in the inner layers of tunica region, while the outer layers undergo anticlinal division.

Several theories have been proposed to explain the organisation and development of shoot apex. There are two views related to shoot apex organization in angiosperms. According to one the apex is a stratified region having distinct cells composed of one or more superficial layers that extend in the meristem region and also enclose subsurface region. The outer cell layers constitute tunica and undergo surface growth. **Tunica** is composed of cells that have a common orientation and undergo anticlinal divisions. In these cells the walls separating the two daughter cells is formed at right angles to the surface. The number of layers comprising the tunica can vary during different stages of development and with the species. Generally the tunica is two –three layered with layers from outside to inside referred as L_1, L_2, L_3 and so on. The epidermis and the young surface layer are derived from the outer L_1 layer. The inner layers of the tunica give rise to corpus eventually forming the ground

tissue and further differentiation into vascular tissue (Fig. 2.5). The subsurface mass of cells is referred as **corpus**. It undergoes divisions in various planes (anticlinal and periclinal). Because of difference in rate and planes of cell division, the tunica and the corpus regions remain histologically distinct and segregated. The apex maintains a layered organization.

The second interpretation is based on cytologically and histologically defined zones. This is referred as cytohistological zonation and this has been regarded as the fundamental feature of the vegetative shoot apex and is seen during all stages of plant development from embryo to an adult individual.

The boundaries in actively dividing cells have been distinguished on the basis of cell size, shape, degree of vacuolation and plane of cell division. Initial zone called the **central zone** represents a conspicuous group of enlarged initial cells located at the stem apex. The cells undergo less frequent division, possess prominent nuclei and are highly vacuolated. This zone functions as the source of all other cells of the apex. The **peripheral zone** flanking it is derived from the central zone and encircles the apical region. The cells of the peripheral zone are smaller, mitotically active and possess dense cytoplasm. They form the sites of origin of cortex and leaf primordial which arise in ordered ontogenic patterns. The third zone known as the **transition or rib zone** is located at the base of apical meristem. This zone is supposed to arise from the central zone and lies as intermediate region between the initial cells and partially differentiated derivative cells below. The cells in this zone are arranged in longitudinal files as a result of cell division occurring at right angles to the stem axis. The cells of this zone form the central pith of the stem after the cells undergo elongation and expansion. Plants lacking the rib zone possess shortened internodes and congested leaves produced in rosettes.

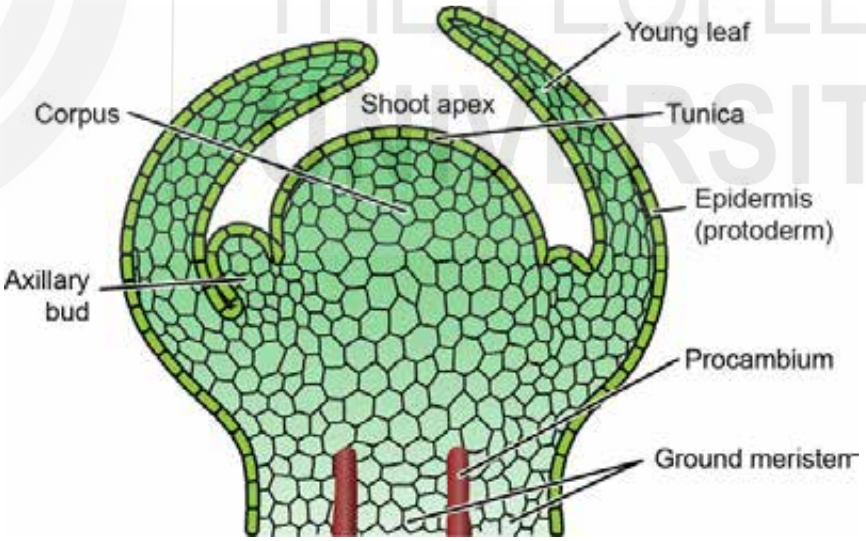

Fig. 2.5: Diagrammatic representation of L.S. of shoot apex.

2.6.1 Apical Cell Theory

The theory was proposed by **Nageli** in 1878. It suggests the presence of single tetrahedral apical cell in the shoot apex in most of the vascular cryptograms. According to this theory a single apical cell is the structural and functional unit of the apical meristem. This cell regulates the whole process of growth. This theory holds true for many algae, majority of bryophytes and pteridophytes.

2.6.2 Histogen Theory

This theory was proposed by **Hanstein** in 1868. According to this theory, three meristematic zones have been recognized in the shoot apex of the angiosperms. Each layer possesses a unique set of initials and these layers are referred as **histogens** (Fig.2.6). The outermost histogen is termed as **dermatogen**. The middle one is referred as **periblem** while the innermost is called as **plerome**. Each histogen performs a definite function. The dermatogen gives rise to epidermis, the periblem gives rise to cortex while the plerome gives rise to vascular cylinder. Later studies revealed that these histogens have no specific morphological function to perform. The theory failed because in most of gymnosperms and angiosperms these three layers could not be distinguished.

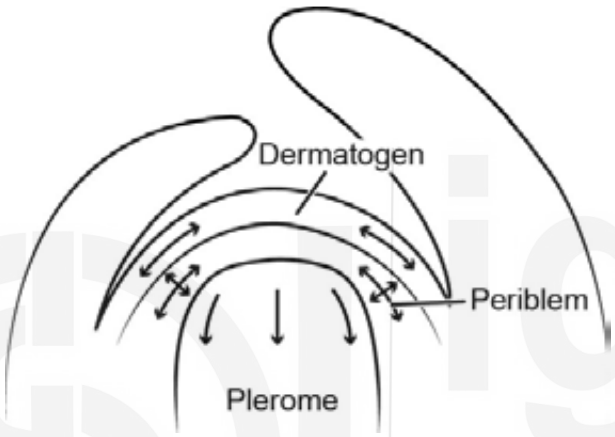

Fig. 2.6: Shoot apex organizations as proposed by Hanstein.

2.6.3 Tunica-Corpus Theory

The theory was proposed by **Schmidt** in 1924. The theory proposed that there are two distinct zones occurring in the shoot apex of the angiosperms. The peripheral layer consists of one or more layers of irregularly arranged cells named as **tunica** (Fig. 2.7). The inner core of cells surrounded by tunica form the **corpus**. The two divisions can be distinguished on the basis of plane of cell division. Tunica region comprises of cells characterized by anticlinal division, the cells of the corpus region divide in various planes. This theory does not provide any correlation between layers and formation of tissues. Tunica and corpus layer possess separate initials. These cells are identified by their larger size, vacuolated contents. The number of initials in two zones varies from species to species. The variations in number of tunica layers occurring in different species or even members of same species at different stages of development of shoot apex could result from plastochron periodicity (Schmidt 1924, Reeve, 1942). Hare (1962) noted three to seven layers in the tunica region in *Daphne pseudo-mezerum*. These layers could be attributed to the seasonal growth changes. In some dicotyledonous families such as Malvaceae, Lauraceae the outer layers of the corpus are uniform and resemble those of tunica. The stratified cells that sometimes show periclinal divisions have been considered part of the corpus. Thus the concept become more flexible as the two regions which are treated as morphological entities are subject to fluctuations.

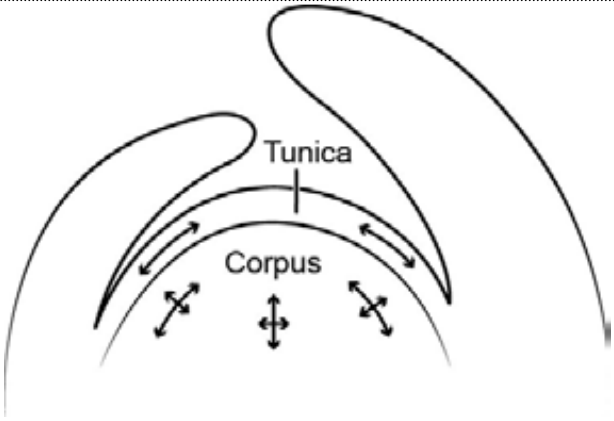

Fig. 2.7: Representation of the shoot apex according to Tunica corpus concept.

2.6.4 Tissue Differentiation Theories

The theory was proposed by **Dermen** in 1947. According to this theory the terms tunica and corpus were replaced and referred as **primary histogenic layers**. He recognized three histogenic layers as **L-1**, **L-II** and **L-III** (Fig. 2.8). These three layers exist in various levels of ploidy in the shoot apex. Example- the cells of the L-I may be diploid (2x), those of L-II may be 2x and those of L-III may be 4x. The constitution in terms of ploidy will be 2, 2, 4. The various other combinations such as 2-2-2, 4-2-2, 2-4-4, 4-4-4 and 2-4-2 have also been reported. The epidermis is derived from L-I. The layer L-II forms one to three layered hypodermis in stem or some portion of cortex and vascular tissue in some species. Generally the vascular tissue and pith originate from L-III. This theory has been considered as modified version of Hanstein's theory.

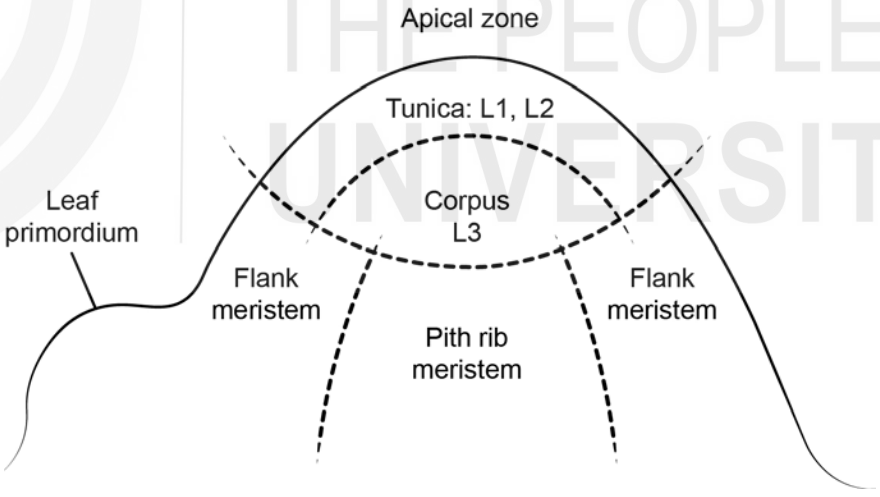

Fig. 2.8: Representation of the shoot apex according to Histogen layer concept.

Mantle Core Concept

This concept was proposed by **Popham and Chan** in 1950. They differentiated the shoot apex into two histological zones without considering the plane of division. The **mantle** included the outer layers of the apex and tunica comprised of the layer of cells from mantle which divide anticlinally. The mass of cells surrounding the mantle is called as **core**. Mantle represents the dome-shaped outer layers of the apex, and the core represents the inner cell mass covered by the mantle (Fig.2.9). In this concept the term 'mantle' is used for tunica and the 'core' is used for corpus.

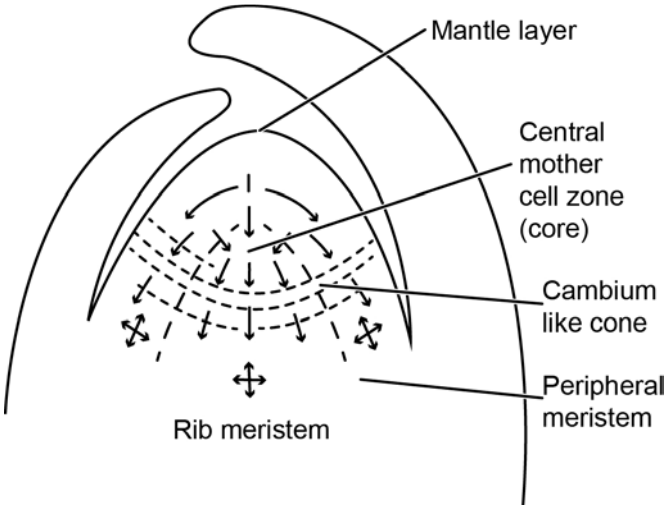

Fig.2.9: Representation of shoot apex according to Mantle-Core concept.

Promeristem (Primordial Meristem) Theory

It consists of three components that include:

- **Protoderm**: forms the epidermis in stem and piliferous layer in the root. It is located at the outermost layer.
- **Ground meristem**: forms the cortex and the pith. It is located at the centre, (between protoderm and procambium).
- **Procambium**: mainly include primary phloem and primary xylem.

Anneau initial or *meristeme d'attente* theory

The theory of apical organisation is based on Plantefol's theory of phyllotaxy and put forward by **Buvat** (1952, 1955). The theory was supported by several subsequent French workers. According to this theory, the peripheral and subterminal regions are initiation zones. The distal groups of cells are inert and do not shows any histogenic function. The three zones recognised in the apical meristem are ***aaneau* initial** (the peripheral active zone), ***meristeme d'attente*** (the meristem that gets activated during the formation of inflorescence or flower), and ***meristeme medullaire*** (central pith region). These layers show correlation with the tunica and corpus region. The distal inactive zone show changes in nucleus size, degree of vacuolation, presence of protein, DNA.

The theory became non-acceptable because the centrally situated cells (*meristems d' attente*) have been referred as waiting meristem which was previously considered as apical initials. It has been noted that apices which remain in the vegetative cover show changes in the zonation, functioning and appearance of *anneau* initial and *meristeme d'attente.* These changes occur in the conditions intermediate between the vegetative and reproductive phases.

Tissue differentiation theory

Three primary meristematic tissues have been recognised in undifferentiated region behind the apical meristem. These undifferentiated tissues are derived from various cell groups or zones of the apex which mature into primary tissues of the shoot. The outermost single layer of cells at the apex is

protoderm and this layer matures into the epidermis of the primary plant body. The procambium also called provascular tissue includes strands of elongated cells that connect to plants mature vascular tissue and differentiate into primary vascular tissues namely primary xylem and primary phloem. Some procambial strands extend into the developing leaf primordial. Procambium has matured into primary xylem and phloem. Some of the procambium also develops into leaf primordial. The remaining cells of the apex form the ground meristem. This meristem is located between the protoderm and procambial strands and fills the center of the axis. It matures into cortex and pith of the plant axis.

Cytohistological zonation theory

The shoot apex of gymnosperms cannot be interpreted in terms of tunica corpus theory. This is because it do not possess layer of cells that divide anticlinally. **Foster** (1939) interpreted the shoot apex of *Ginkgo biloba* in terms of certain regions or zones which possess distinct cytological characteristics. These zones have a relationship with the growth processes in the apex. The four growth zones have been recognised by him are given below:

- **Apical initial group** - this includes group of initials along the apical surface along with some lateral or sub-adjacent derivatives.
- **Central mother cell zone** - This zone lies below the apical initial group and is derived from it. The distal group of cells is lightly stained, vacuolated and show slow activity. The primary walls of the central mother cells are thick walled and pitted.
- **Rib meristem -** It consist of centrally located central mother cells and give rise to pith. The cells are vacuolated and divide transversely to form vertical files. This zone is also called as file or pith meristem.
- **Peripheral meristem (flank meristem)** - This zone originates from the lateral derivatives of the apical initials and partly from the central mother cells. The cells are densely stained and mitotically active. The activity of this zone leads to the formation of leaf primordial (Fig. 2.10). The periclinal divisions in this zone cause elongation of the shoot while anticlinal divisions increase the width.

The four zones are morphologically and biochemically distinct. This type of zonation has been noted in number of angiosperms. The shoot apices of angiosperm exhibit cytohistological zonation in addition to tunica corpus zonation.

Four zones are recognised namely:

i) **Tunica initials**-that consist of an apical group of cells,

ii) **Corpus initials**-those occur below apical initials and are similar to central mother cells,

iii) A **peripheral zone**, and

iv) A **rib meristem** (Fig. 2.10).

Tunica initials contribute cells to central mother cell zone and to peripheral meristem. The central mother cell zone donates cells to the rib meristem and pith. The peripheral meristem is highly meristematic and leaf primordia originate from this layer.

In addition, Popham and Chan (1950) described a fifth zone occurring just below the leaf primordium. It is cup shaped and located between the central mother cells, rib and flank meristem. It is called as cambium like zone. It is not a universal feature but is reported in few species such as *Livistona, Bellis perennis, Chrysanthemum morifoilum* and *Ricinus communis*. This zone is short lived and develops during the mid plastochron and disorganizes.

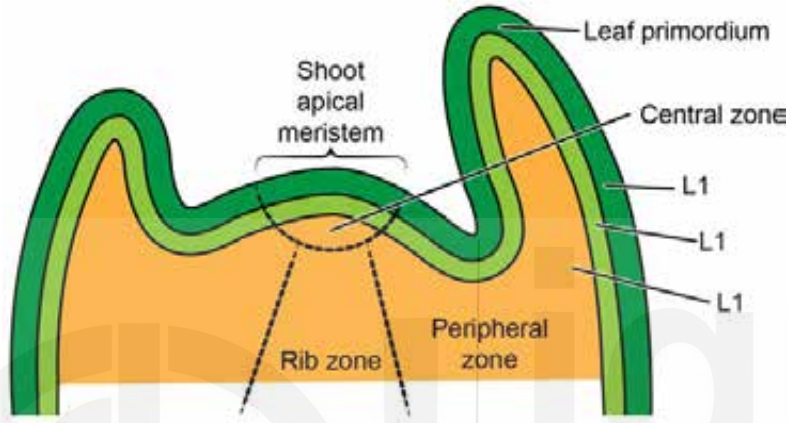

Fig.2.10: Shoot apices of angiosperm showing cytohistological zonation.

SAQ 3

a) Fill in the blanks.

i) In shoot apex organization the peripheral layer consists of one or more layers of irregularly arranged cells forming the ……. region.

ii) …… meristem is located on the lateral side of the stem and root.

iii) The fourth histogen which produced root cap in monocots is known as …….. .

iv) …….. layer of shoot apex forms the base of the epidermis.

v) Terminal position in the root is occupied by …….... .

b) Define the following terms:

i) Tunica

ii) Corpus

iii) Mantle

iv) Protoderm

v) Dermatogen

c) Fill in the blanks.

i) In shoot apical meristem the inner zone is known as …….. .

ii) When tunica zone is made up of two or more layers of layers it is called …….. .

iii) The third zone located at the base of apical meristem is known as …….. .

iv) Unique set of initials present in the layers are referred as ……. .

v) Popham and Chan in 1950 proposed the ……. concept.

2.7 SUMMARY

- Apical meristems are located terminally in plants i.e. growing tips of root and shoot. All the primary tissues originate from this meristem. Lateral meristem is present on the lateral side of the stem and root. These meristems lie between the regions of the permanent tissue and give rise to secondary permanent tissues. These meristems help in increasing the thickness of the plants. Example- vascular cambium and cork cambium.
- Intercalary meristem lies between the regions of permanent tissues. It is found either at the base of leaf or at the base of internodes. This meristem increases length of the internode.
- The root apical meristem is subterminal in position. The cells present in the region are densely cytoplasmic and undergo active division. The mature tissues of the root are derived from these cells or initials. The root apex is enclosed within the structure called root cap.
- Different theories have been proposed by several workers to depict the structure and organization of the root apical meristem. The apical cell theory proposed by Nageli (1858) suggests that divisions in a single apical cell give rise to root in vascular cryptograms. The upper side of the apical cell gives rise to body of the root while the basal helps in root cap formation. In flowering plants, a group of initials participate in the formation of the root structure. Histogen theory proposed by Hanstein (1868) suggests the existence of three layers of meristems (or histogens) in the root apex. The dermatogen gives rise to epidermis, periblem gives rise to cortex while plerome forms the vascular cylinder of the mature root. Haberlandt (1914) proposed the names protoderm, ground meristem and procambium for these three layers. Later on Schüepp (1917) proposed that root apex is organized in terms of planes of division i.e. kooper-kappe theory concept of root apex organization.
- Root cap occupies terminal position in the root. In dicotyledons it arises from initials that give rise to epidermis. A central cup like region of cells lying between the root cap and the active meristematic region. The cells present in this region possess low concentration of DNA, RNA and protein. The cells of this region do not synthesise DNA. This inactive region of the root is called as quiescent center.

- Shoot apical meristem is located at the terminal position of the shoot. It lies immediately above the leaf primordium. Several theories have been proposed to explain the mode of development of shoot apical meristem. **Apical cell theory** proposed by Nageli (1878) suggests presence of single tetrahedral apical cell in the shoot apex in most of the vascular cryptograms. **Histogen theory** proposed by Hanstein (1868) recognises presence of three meristematic zones in the shoot apex of angiosperms. Each layer possesses a unique set of initials and these layers are referred as histogens. The outermost histogen is dermatogen, middle one is referred as periblem while the innermost is called as plerome. Each histogen performs a definite function. The dematogen gives rise to epidermis, the periblem gives rise to cortex while the plerome gives rise to vascular cylinder. The theory failed because in most of gymnosperms and angiosperms these three layers could not be distinguished.

- Tunica-corpus theory proposed by Schmidt (1924) suggests the presence of two distinct zones in the shoot apex of angiosperms. The peripheral layer consists of one or more layers of irregularly arranged cells named as **tunica**. The inner core of cells surrounded by tunica form the **corpus**. The two zones can be distinguished on the basis of plane of cell division. Tunica region is comprises of cells characterized by anticlinal division, the cells of the corpus region divide in various planes. The concept becomes non-acceptable because of fluctuations.

- Popham and Chan (1950) introduced the **mantle-core hypothesis**. The mantle included the outer layers of the apex and tunica comprised of the layer of cells from mantle which divide anticlinally. The mass of cells surrounding the mantle is called as **core**.

2.8 TERMINAL QUESTIONS

1. Describe in brief the main points of the root apex organization according to Histogen theory.
2. Elaborate the tunica corpus organization of shoot apex in plants.
3. Enlist the salient features of *anneau* initial or *meristeme d'attente* theory.

2.9 ANSWERS

Self-Assessment Questions

1. a) **Shoot apical meristem** - It is located at the terminal position of the shoot. The cells in the region divide continuously to form new tissues and organs. This part lies immediately above the leaf primordium. It is variable in shape at different stages of plant development. It is usually radially symmetrical and appears to be more or less convex in a median longitudinal section.

   Root apical meristem - It is located at the apex of the root. It is subterminal in position. The mature tissues of the root are derived from these cells or initials. The root apex is enclosed within the structure called rot cap.

b) **Vascular cambium -** It is a lateral meristem that extends throughout the length of the plant from the tips of the shoots to the tips of the roots. The cells of vascular cambium produce secondary tissues after division. It is present in all perennial and in some annual plants.

Cork cambium (phellogen) -They are found in the bark of roots and stems of woody plants and produce cork cells. In trees they are produced as long cylinders running parallel to the vascular cambium.

c) **Apical meristem -** These are located at the apices or growing points/tips of root and shoot. All the primary tissues originate from this meristem. Cell divisions and subsequent cell enlargement in these areas lengthen the above and below ground parts of the plant.

Lateral meristem - The meristem lies on the lateral side of the stem and root. The cells are arranged parallel and normally divide periclinally or radially and give rise to secondary permanent tissues. These meristems help in increasing the thickness of the plants. The vascular cambium and the cork cambium are good examples of this meristem.

Intercalary meristem - It is found either at the base of leaf or at the base of internodes. It lies between the regions of permanent tissues. It helps in increasing the length of the internode. Grasses have intercalary meristems located along the stems near the nodes.

2. a) i) shoot apical meristem

ii) lateral meristem

iii) apical cell theory

iv) Hofmeister (1852)

v) Histogen theory

vi) Korper-Kappe theory

b) i) **Root cap :** Root cap occupies terminal position in the root. If the root cap is removed the cells of the quiescent center divide rapidly to form new root cap. The outer walls of the root cap are mucilaginous and help to reduce friction between apex of the root and hard soil during root penetration in the soil.

ii) **Quiescent center :** A central cup like region of cells lying between the root cap and the active meristematic region is referred as quiescent center. The cells present in this region possess low concentration of DNA, RNA and protein. This is inactive region of the root since the cells of this region do not synthesise DNA. This region has been recognised in root tip

of large number of plants. It is generally hemispherical in shape and contains several hundred cells. The cells of the quiescent center become active whenever the previous initials are damaged. Thus the center acts as the reservoir of cells resistant to the damage because of their inactive nature.

iii) **Vascular cambium :** This tissue extends throughout the length of the plant from the tips of the shoots to the tips of the roots. It is present in all perennial and in some annual plants. The cells of vascular cambium produce secondary tissues after division.

3. a) i) tunica

ii) lateral

iii) calyptrogens

iv) dermatogens

v) root cap

b) i) **Tunica :** It is zones occurring in the shoot apex of the angiosperms. The peripheral layer consists of one or more layers of irregularly arranged cells named as tunica. Tunica region comprises of cells characterized by anticlinal division

ii) **Corpus :** It is a zone of cells occurring in the shoot apex of the angiosperms. The inner core of cells surrounded by tunica form the corpus. The cells of the corpus region divide in various planes.

iii) **Mantle :** It is one of the histological zones of the shoot apex. The mantle included the outer layers of the apex and tunica comprised of the layer of cells from mantle which divide anticlinally.

iv) **Protoderm :** It is one of the three meristematic zones or histogens rocognized in the shoot apex of the angiosperms. Each layer possesses a unique set of initials. Protoderm is the outermost layer forming the epidermis in stem.

v) **Dermatogen :** It is one of the three meristematic zones or histogens recognised in the root apex of the angiosperms. Each layer possesses a unique set of initials. The dermatogen is the outermost layer that gives rise to epidermis of the mature root.

c) i) corpus

ii) multistratose

iii) transition or rib zone

iv) histogens

v) Mantle core

Terminal Questions

1. Histogen theory was proposed by Hanstein in 1868. The theory suggests the existence of three layers of meristems or histogens in the root apex. These include dermatogens, periblem and plerome. Each layer has a specific function. The dermatogen gives rise to epidermis, periblem gives rise to cortex while plerome forms the vascular cylinder of the mature root. Later on **calyptrogen** was designated as the fourth histogen which produced root cap in monocots. Later on Haberlandt in 1914 proposed the names protoderm, ground meristem and procambium for these three layers respectively.

2. According to Schmidt (1924), two distinct zones occur in the shoot apex of the angiosperms. The peripheral layer consists of one or more layers of irregularly arranged cells named as tunica. The inner core of cells surrounded by tunica form the corpus. The two divisions can be distinguished on the basis of plane of cell division. Tunica region is comprises of cells characterized by anticlinal division, the cells of the corpus region divide in various planes. Tunica and corpus layer possess separate initials. These cells are identified by their larger size and vacuolated contents. The number of initials in two zones varies from species to species. The variations occur in number of tunica layers occurring in different species or even members of same species at different stages of development of shoot apex. Three to seven layers in the tunica region has been noted in *Daphne pseudo-mezerum*. These layers could be attributed to the seasonal growth changes. In some dicotyledonous species such as Malvaceae, Lauraceae the outer layers of the corpus are uniform and resemble those of tunica.

3. The theory of apical organization is based on Plantefol's theory of phyllotaxy and put forward by Buvat (1952, 1955). According to this theory, the peripheral and subterminal regions are initiation zones. The distal group of cells is inert and does not show any histogenic function. The three zones recognised in the apical meristem are ***aaneau* initial** (the peripheral active zone), ***meristeme d'attente*** (the meristem that gets activated during the formation of inflorescence or flower), and ***meristeme medullaire*** (central pith region). These layers show correlation with the tunica and corpus region. The theory became non-acceptable because the centrally situated cells (*meristeme d' attente*) have been referred as waiting meristem which was previously considered as apical initials. Several other workers have shown that central *meristeme d'attente* is capable of dividing actively and giving rise to a vegetative shoot under certain conditions.