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1. Details of Module and its Structure

Module Detail	
Subject Name	**Botany**
Paper Name	Plant Development
Module Name/Title	Meristem
Module Id	
Pre-requisites	
Objectives	**To study** Meristem, its significance, and its regulation
Keywords	Meristems, Tissues, Shoot apex, Root apex, Apical Cell Theory, Shoot Apical Meristem, Apical dominance, Histogen Layer Theory, Histogen Theory, Korper-Kappe Theory, Mantle-Core Theory, Tunica Corpus Theory, Dehydroascorbate, Floral meristem, Oxidized Glutathione, Rduced Glutathione, Phytohormones, Quiscent Centre, Reactive Nitrogen Species, Reactive Oxygen Species, Reduced Ascorbate,

Structure of Module / Syllabus of a module (Define Topic / Sub-topic of module)	
	Fertilization
<Topic name2>	**Meristem:** Types of meristems in plant development; Structural organization of the meristems; Maintenance of non-differentiated states.

2. Development Team

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Meristem: Types of meristems in plant development; Structural organization of the meristems; Maintenance of non-differentiated states.

1. Introduction:

All organisms are made up of cells. They may be unicellular or multicellular. Organisms start their life cycle from the unicellular stage. Growth is essentially an irreversible increase in cell number and consequently an essential increase in the dry mass of organisms. Growth takes place up to a certain period of life cycle, either by increasing the size of individual cells or by increasing the cell number or by both. Further, organisms have the impressive ability to regenerate damaged parts. In the case of higher plants, increasing shoot length makes the plant taller, thus allowing it better access to sunlight for photosynthesis while increase in root length enables a plant to tap better into the water and mineral sources of soil. Many plants also increase the diameter of their roots and stems.

Plant growth occurs in areas called meristems that are the site of repeated cell division of unspecialized cells. These cells differentiate and become specialized in relation to the function they have to perform. These cells are similar in origin but multipotent, i.e. they can give rise to different groups of cells. Individual group of cells are similar in function and are functionally associated to each other. Such group of cells is called as permanent tissues.

1.1 Meristems

Almost all tissues starts to divide from some incipient cells, called as meristems or meristematic cells. Early phased meristematic cells are also called as promeristems or constructive tissue. Unlike other cells of plants, meristematic cells remain totipotent. They play an important role in the formation of new tissues and in the correct placement of those tissues within the plant body. This process is called as pattern formation. These play a pivotal role in normal plant growth. They are also the source of the regenerative potential of a plant after injury.

Meristematic cells have following properties:

1. These are found in the vegetative part of the plants.
2. They are living (lack non-living substances or inclusions) and of thinner wall (having primary cell wall only), isodiametric cells.
3. The cells are small and their protoplasm fills the cell completely. They have prominent nucleus (positioned in the centre) and either they lack vacuole or vacuoles are extremely small. The cytoplasm does not contain differentiated plastids (chloroplasts or chromoplasts), although they are present in rudimentary form (proplastids).
4. These cells are either dividing or about to divide or have potential to divide.
5. They lack intercellular spaces in between them.
6. These cells are metabolically more active and grow as long as they are alive.

2. Classification of Meristematic Tissues

Meristematic tissues are variously classified, on the basis of their growth, plane of division and position and function etc.

2.1 Classification of meristematic tissues on the basis of origin and development:

On the basis of origin, meristematic tissues have been divided into three categories:

(a) Promeristem or primordial meristem: Promeristem or primordial meristem is the embryonic stage of developing meristems and represents the primary phase of the meristem of a growing plant. Promeristems are the young growing points of meristems, situated on the apices of roots and shoots. They are the sites of active mitotic division. Promeristem gives rise to primary meristems.

(b) Primary meristem: Primary meristems develop from promeristems. Such type of tissues is found on the apical and intercalary regions of shoots and roots. Their cells are also in the continuous phase of division. The cells of primary meristems give rise to primary permanent tissues.

(c) Secondary meristem: Initially, these types of tissues are not present but, if required, develop in the later stages by acquiring potential to divide in some of the primary permanent tissues, e.g., interfascicular and cork cambium of roots. Secondary meristems form secondary permanent tissues.

2.2 Classification of meristematic tissues on the basis of position:

On the basis of position, meristematic tissues have been divided into three categories (Fig. 1):

(a) Apical Meristem

These meristems are situated on the apices of roots and shoots. Roots and shoots increase in their lengths by the continuous division of these tissues. These meristems form the growing point on the apices of growing point.

(b) Intercalary Meristem

Actually, they are the regions separated from the apical meristems at the time of growth of the shoot and do not change into permanent tissues and remained included as meristematic tissues in between permanent tissues. Intercalary meristems are capable of cell division and allow for rapid growth of many monocots. Intercalary meristems at the nodes of bamboo promise rapid stem elongation, while those at the base of most grass leaf blades assure damaged leaves to rapidly grow. Horsetails (*Equisetum*) and *Mentha* also exhibit intercalary meristems.

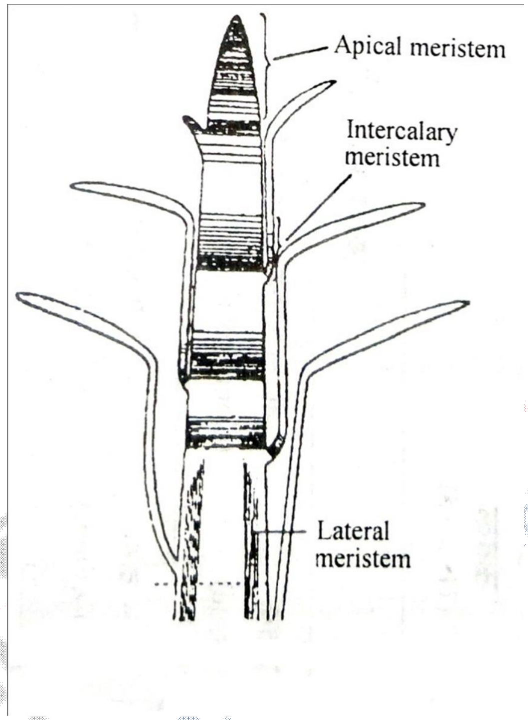


Fig. 1. Meristems, according to the position.

(c) Lateral Meristem:

These meristems are situated in lateral parts of stems and roots. Lateral meristems are responsible for the secondary growth in stems and roots increasing their girth. For example, vascular cambium and cork cambium of the perennial plants, formed after redifferentiation in permanent tissues.

2.3 Classification of meristematic tissues on the basis of plane of division

There are three types of meristems on the basis of plane of division:

(a) **Mass meristem:** Its cells divide in all directions resulting into irregular organogenesis. These meristems are seen in primary developmental phase of embryo and endosperm.

(b) **Plate meristem:** Its cells divide anticlinally (i.e. at an angle of 90º) and form plate like structure resulting into plate like tissue formation. These meristems are involved in the formation of epidermis and multiliner blade of flat pinna.

(c) **Rib meristem:** Its cells always divide in anticlinal manner due to which rows of cells are formed at longitudinal axis. These meristems form pro-meristem to cortex and pith in roots and stems.

2.4 Classification of meristematic tissues on the basis of function:

(a) **Protoderm:** This type of meristem is situated on outer layer and develops into the epidermis.

(b) **Procambium:** It lies just inside the protoderm and its cells are elongated and form primary vascular bundles. It develops into primary xylem and primary phloem. It also produces the vascular cambium, cork cambium and secondary meristems. The cork cambium further differentiates into the phelloderm (to the inside) and the phellem, or cork (to the outside). All three layers (cork cambium, phellem and phelloderm) constitute the periderm. In roots, the procambium can also give rise to the pericycle, which produces lateral roots in eudicots.

(c) **Ground tissue:** Its cells are comparatively large, thin walled and isodiametric. Division of these cells gives rise to epidermis, cortex, endodermis, pericycle, medullary rays and medulla. These meristems are responsible for primary growth, or an increase in length or height.

(d) **Secondary meristems:** These are also called as the lateral meristems because they surround the stem of a plant and stems grow laterally due to their activity (i.e., enlarge in girth by producing secondary xylem and secondary phloem). Secondary meristems produce wood in trees and give them arborescent habit. Secondary meristems do not occur in herbaceous plants. Cork cambium is also a kind of secondary meristem, which gives rise to the periderm by replacing the epidermis.

3. Shoot Apical Meristem (SAM)

3.1 Organization of SAM

In higher plants, the shoot apical meristem (SAM) gives rise to all the above-ground organs. It is supposed to be the site of organogenesis in flowering plants. It contains all the necessary information of shoot building and its pattern formation in the form of cell signalling. The SAM supplies cells that divide and differentiate to form the elements of the shoot. It also initiates the lateral organ formation and decides their anatomical features and cell division patterns. Primordia of leaves, sepals, petals, stamens and ovaries are initiated at SAM. First indication of flower development appears in the form of loss of the apical dominance.

The SAM gives rise to:

(a) **Central zone:** It is located in the center of the SAM and acts as a pool of undifferentiated, indeterminate cells. Cells of this zone have a stem cell (initial cell) function and are essential for meristem maintenance. Here the cell division is less frequent.

(b) **Peripheral zone:** This zone flanks the SAM, its cells divide more frequently and are incorporated into leaf primordia.

(c) **Rib zone:** It is the proximal region. It supplies the cells that form the body of the stem.

Although all the tissues of shoot originate from shoot apex, despite of this, the organization of shoot apical meristem differs from plant to plant.

Different workers tried to explain the structure of organization of apical meristems differently. Wardlaw (1957) explained following 5 regions in shoot apical meristems (Fig. 2):

(a) **Distal region:** This is the apical most region of SAM and is made of meristematic cells arranged in one or many rows.

(b) **Sub-Distal region:** It is situated just after the distal region. This is also made of meristematic cells. Growing points are situated in this very region.

(c) **Organogenic Region:** The process of leaf initiation and tissue differentiation occurs in this region.

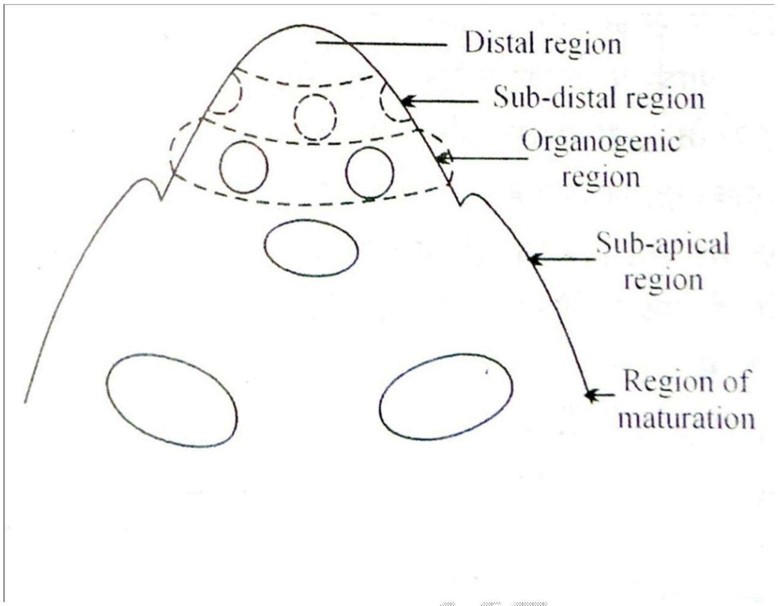


Fig. 2. Shoot apex with different regions, after Wardlaw (1957).

(d) **Sub-apical region:** This region is situated below the organogenic region. Cells of this region constantly dividing and show cell elongation and cellular differentiation.

(e) **Region of maturation:** This region is situated below the sub-apical region. All the cells of this region are mature and neither do they divide or differentiate.

At the same time, the SAM can be viewed in terms of clonally distinct cell layers, viz. L1, L2, and L3. The outermost layer, L1, comprises epidermal cells that divide only anticlinally. Cells in the inner L2 and L3 layers divide both anticlinally and periclinally and give rise to the inner tissues of the leaves and stem.

The above zones are maintained by a complex signalling pathway. In *Arabidopsis thaliana*, 3 interacting genes are required to regulate the size of the stem cell reservoir in the SAM by controlling the rate of cell division.

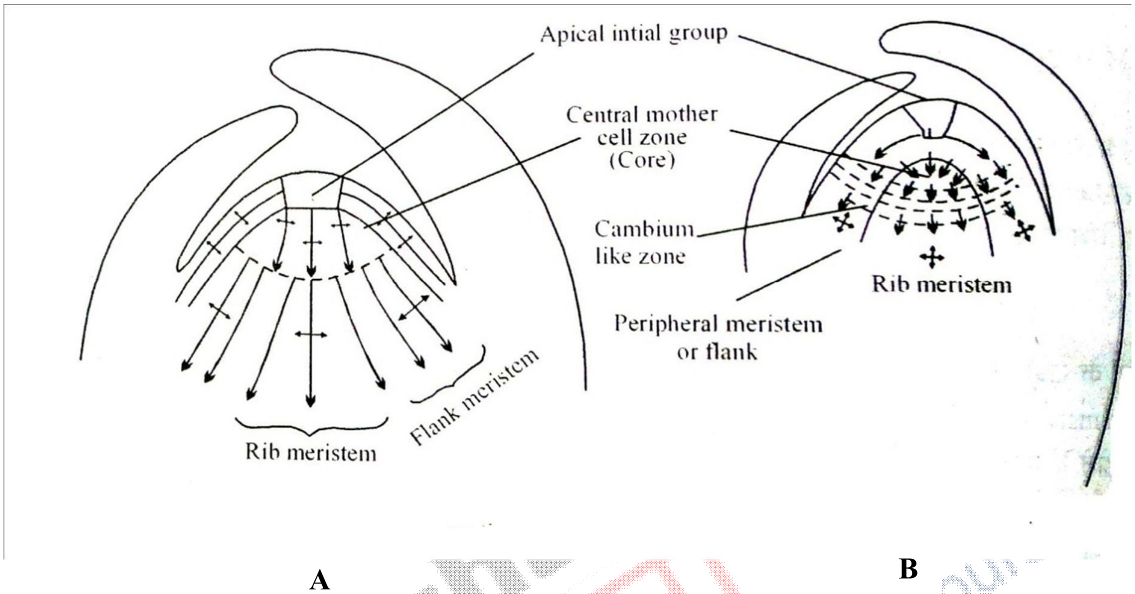


Fig. 3. LS of shoot apex of *Ginkgo biloba* histological zonation (A), Histological zonation in dicot shoot apex (B).

3.2 Gymnospermous shoot apical meristems: Here, cellular organization in different phases of development has not been seen. But, Foster (1939) identified interrelated cellular regions in 4 different regions and named them as (Fig. 3):

(a) Apical initial group

(b) Central mother cell zone

(c) Rib meristem

(d) Peripheral meristem or flank meristem

Further, Propham and Chan (1950) and Singh and Singh (1970) proved a cambium like region below the youngest leaf primordium in *Chrysanthemum morifolium* and *Ricinus* sp., respectively.

3.3 Types of shoot apex: Newman (1965) named the group of permanent initial cells of shoot apex as ócontinuing meristematic residueô (CMR). On the basis of nature of the cells of CMR Newman divided shoot apex into 3 categories (Fig. 4):

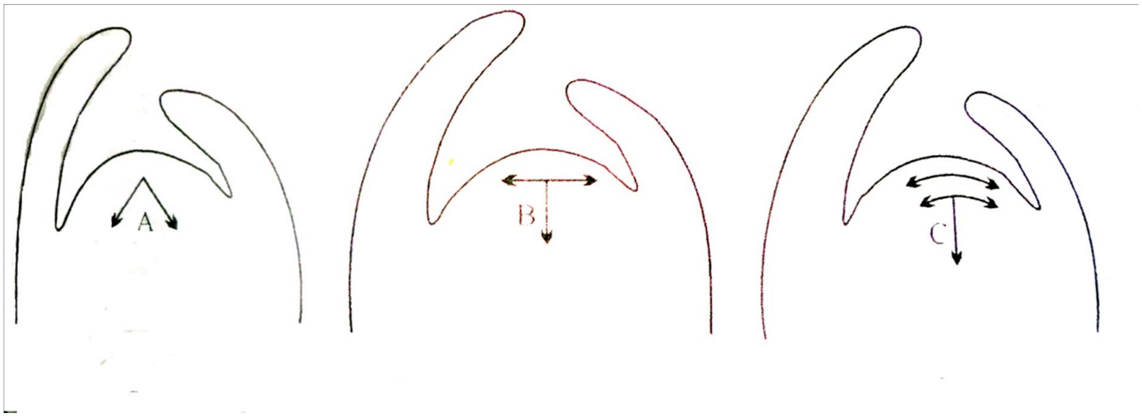


Fig. 4. Types of shoot apex: Monoplex type (A), Simplex type (B), Duplex type (C).

(a) **Monoplex type:** In this type of shoot apex, meristematic tissues are in the form of superficial layer and centered downwards. Only one division is needed for the growth, thereby increase in length and breadth becomes possible.

(b) **Simplex type:** In this type of shoot apex, meristematic cells are parallel sided and divide anticlinaly and periclinaly and give rise to meristematic tissues. They are in the form of superficial layer. The division process is related to one-layered cellular organization. Generally, this type of shoot apex is found in gymnosperms only.

(c) **Duplex type:** In this type of shoot apex, the cells of CMR are parallel sided and at least configured in 2 layers. Upper most layer divides by anticlinal division while subsequent layers divide by anticlinal and periclinal divisions both. These consecutive layers are responsible for growth in length as well as breadth. This type of shoot apex is found mostly in angiosperms.

3.4 Apical dominance in SAM

Supremacy of one SAM to grow and to inhibit the growth of other meristems is called apical dominance. This results the plants to have one clearly defined main trunk. In this way, the tip of the trunk grows rapidly and is not shadowed by branches. If the dominant meristem is cut off, one or more branch tips will assume dominance. After the removal of apical meristem, often the herbaceous plants attain a bushy growth. Gardeners often exploit this behavior of plants to make the plants bushy and to fence their garden called as pruning. The mechanism of apical dominance is based on the plant hormone auxin, produced in the apical meristem and transported towards the roots in the cambium.

3.5 Theories related to shoot apex organization

Multiple theories have been proposed to understand the structure and organization of shoot apical meristem:

3.5.1 Apical Cell Theory:

This theory was proposed by Hofmeister (1957) and elaborated by Nageli (1978). According to this theory, the apical cell of shoot is always in most active state. Various tissues of shoots are formed by the activity of this apical cell. Apical cell of the shoot apex also exhibits differentiation and regulatory function necessary for pattern formation. The apical cell gives rise to new cells by cutting one or two cells on its posterior face. These cells transform into tissues in the later stage (Fig. 5).

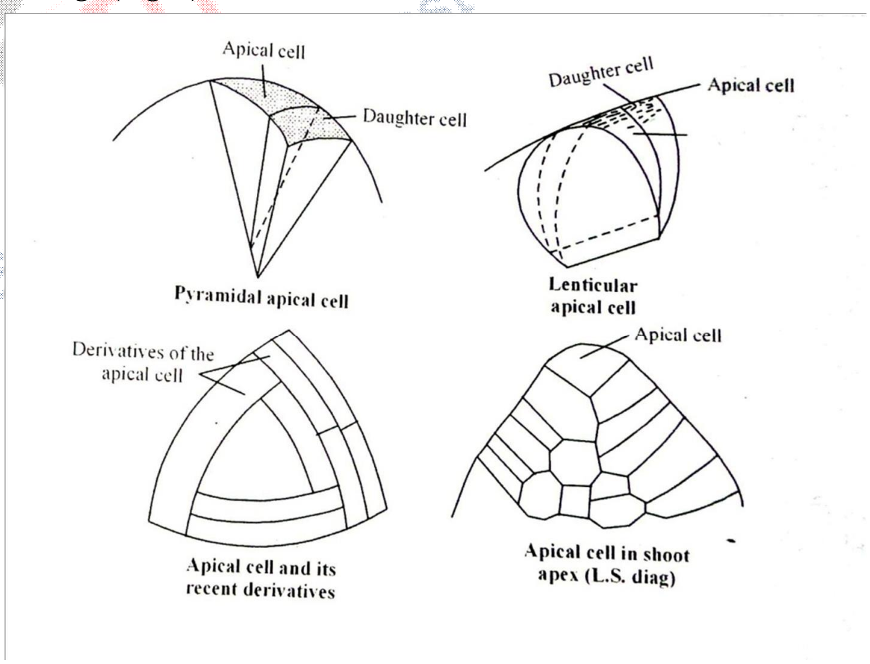
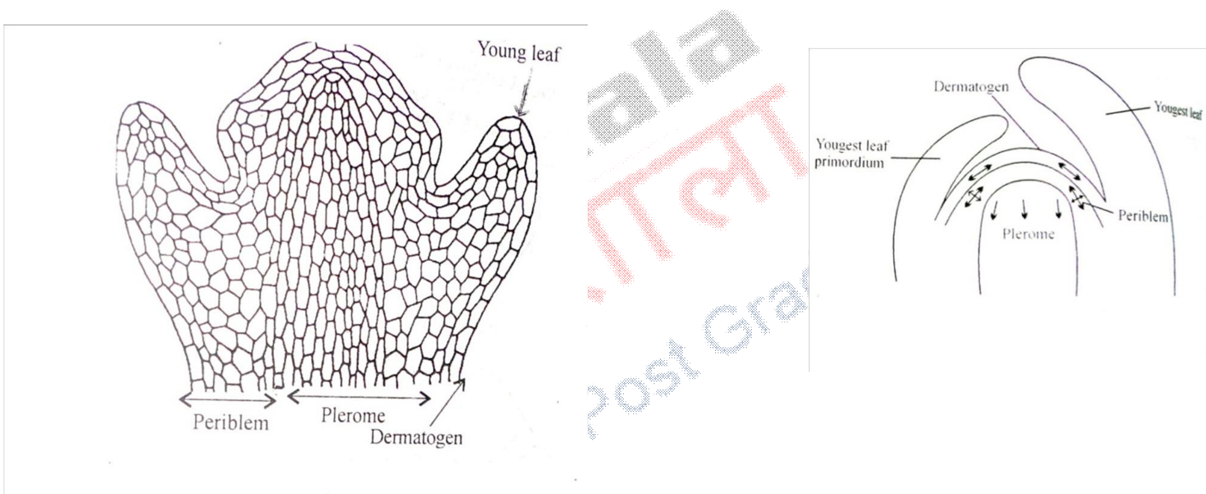


Fig. 5. Apical cell of shoot apex

This theory efficiently explains growth and differentiation process in some higher algae, bryophytes and some pteridophytes, but failed to explain the structure and organization of shoot apex in phanerogams, i.e. gymnosperms and angiosperms, since the shoot apices of phanerogams consist of many cells.

3.5.2 Histogen Theory:

Hanstein (1970) proposed this theory after studying the shoots and embryos of many angiosperms. He identified 3 clear-cut regions in shoots and roots (Fig. 6):



(A) (B)

Fig.6. LS of shoot apex showing histogen layers (A), LS of shoot apex with histogen layers wherein arrows indicate direction of growth (B).

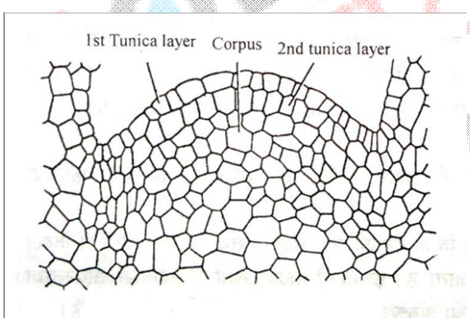
- **(i)** **Dermatogen**: This is the outermost layer of cells. It forms epidermis of the stems.
- **(ii)** **Periblem**: This region is just below the dermatogens. It is unilayered at apical regions but multilayered at lower regions. Division and differentiation of this region gives rise to hypodermis, general cortex and endodermis.
- **(iii)** **Plerome**: This is situated at inner side of periblem and middle part of the shoot apex. This is made of thin layered isodiametric cells. This forms the

stellar tissues, viz. pericycle, primary vascular tissue, medullary rays and medulla. Additionally, it also gives rise to procambium situated at sub-apical region in the shoot.

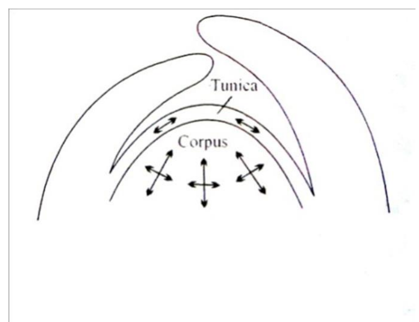
Plerome in the roots performs the similar function as the plerome in shoots.

Histogen theory is not suitable for the explanation of shoot apex because there is no clear-cut demarcation between dermatogens and periblem. Thus, histogen theory is used to explain the growth of the root apices only.

3.5.3 Tunica Corpus Theory: This theory was proposed by Schmidt in 1924 to explain the apical growing regions of shoots only (and not used to explain the growth of root apices). According to this theory, two regions viz. tunica and corpus are found in shoot apical regions. Tunica comprises one or many outer layers of shoot apex. Cells of tunica region are cut only by anticlinal divisions. Tunica expands the surface of shoot apex, and its outer most layer gives rise to epidermal layer. Tunica covers the corpus wherein cells divide in all directions and volume of the shoot increases (Fig. 7).



A



B

Fig. 7. LS of shoot apex showing tunica and corpus (A), LS of shoot apex showing direction of growth (B)

By studying the shoot apex in many angiosperms, it becomes clear that in some special cases, tunica divides by periclinal divisions also along with anticlinal divisions. In monocots, the tunica determines the physical characters of the leaf edge and margin. In dicots, corpus determines the characteristics of the edge of the leaf.

3.5.4 Mantle-Core Theory: Propham and Chan (1950) proposed this theory to explain the division in peripheral tissues in shoot apical regions of some angiosperms. This theory is similar to tunica-corpus theory.

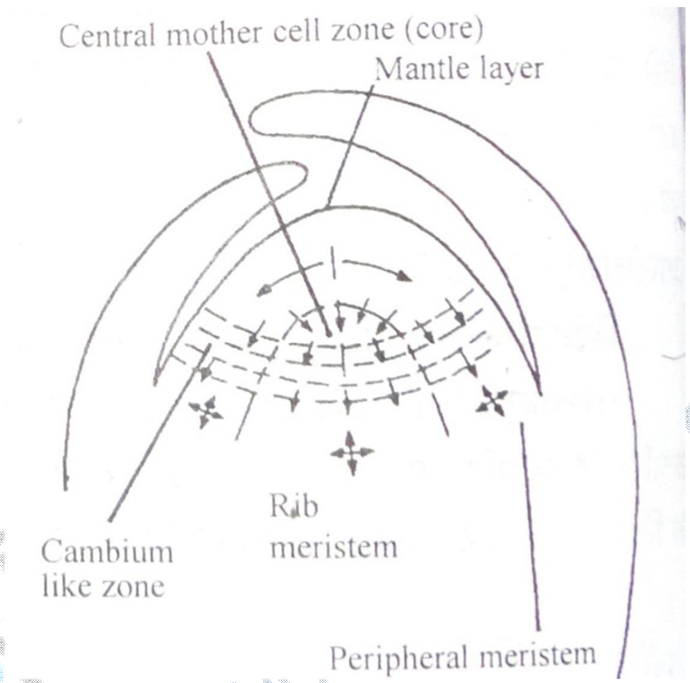


Fig. 8. Scheme of LS of shoot apex, according to Mantle-Core Theory (arrows indicate growth).

This theory does not rely upon the manner by which the cells divide; it only states that mantle is peripheral cellular region of the shoot apex. Mantle covers the central core region (Fig. 8).

3.5.5 Histogen Layer Theory: Dermen (1947) defied tunica-corpus theory and proposed histogen layer theory. According to this theory, shoot apex of angiosperms is organized in 3 layered structure. They may be called as L-I, L-II and L-III. According to this theory, epidermis of leaves and stem develop from L-I; hypodermis, cortex and some of the vascular bundle regions develop from L-II; while vascular tissues and medulla develop from L-III. Organizational form of shoot apex in 3 layers gives this theory a modified version of histogen theory.

4. Root Apical Meristem (RAM)

Root apical meristems (RAM) are the sub-apical region of apical portion of the roots wherein the meristematic cells are situated. They produce different internal tissues of roots. This region has following distinctive features (Fig. 9):

1. It is always sub-terminal region because it is covered by the root cap.
2. Neither any lateral appendage or branch or their growth zone, e.g. leaf or branch primordia are attached to the RAM.
3. It is smaller than the shoot apex.
4. The cells of RAM consistently divide and their activity enables the roots to grow in positively geotropic and negatively phototropic direction.

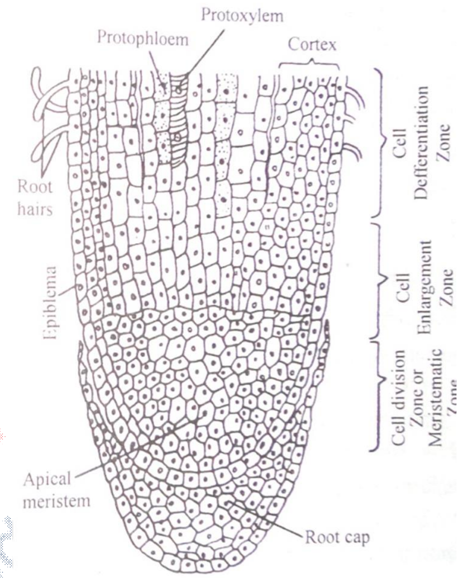


Fig. 9. LS of root apex.

4.1 Organization of Root Apex

Apical cells of the primary roots are meristematic in nature and they attain the capability to divide as soon as the embryonal radical forms. The cells of RAM have bigger and prominent nucleus and have dense cytoplasm, either lack vacuoles or vacuoles are very small. These cells are either ellipsoidal or polygonal and lack inter-cellular spaces. Their cell walls are thin and uniform. They divide to form the cells of mature root system. Root apex is either partially or completely covered with the root cap cells. Root cap cells are fully matured cells which develop from dermatocalyptrogen in dicot plants and calyptrogen in monocot plants. RAM gives rise the cells of the main axis of roots and the root cap initial cells. Tissue system comprised of epidermis, cortex and vascular cylinder is situated behind the root apex (Fig. 10).

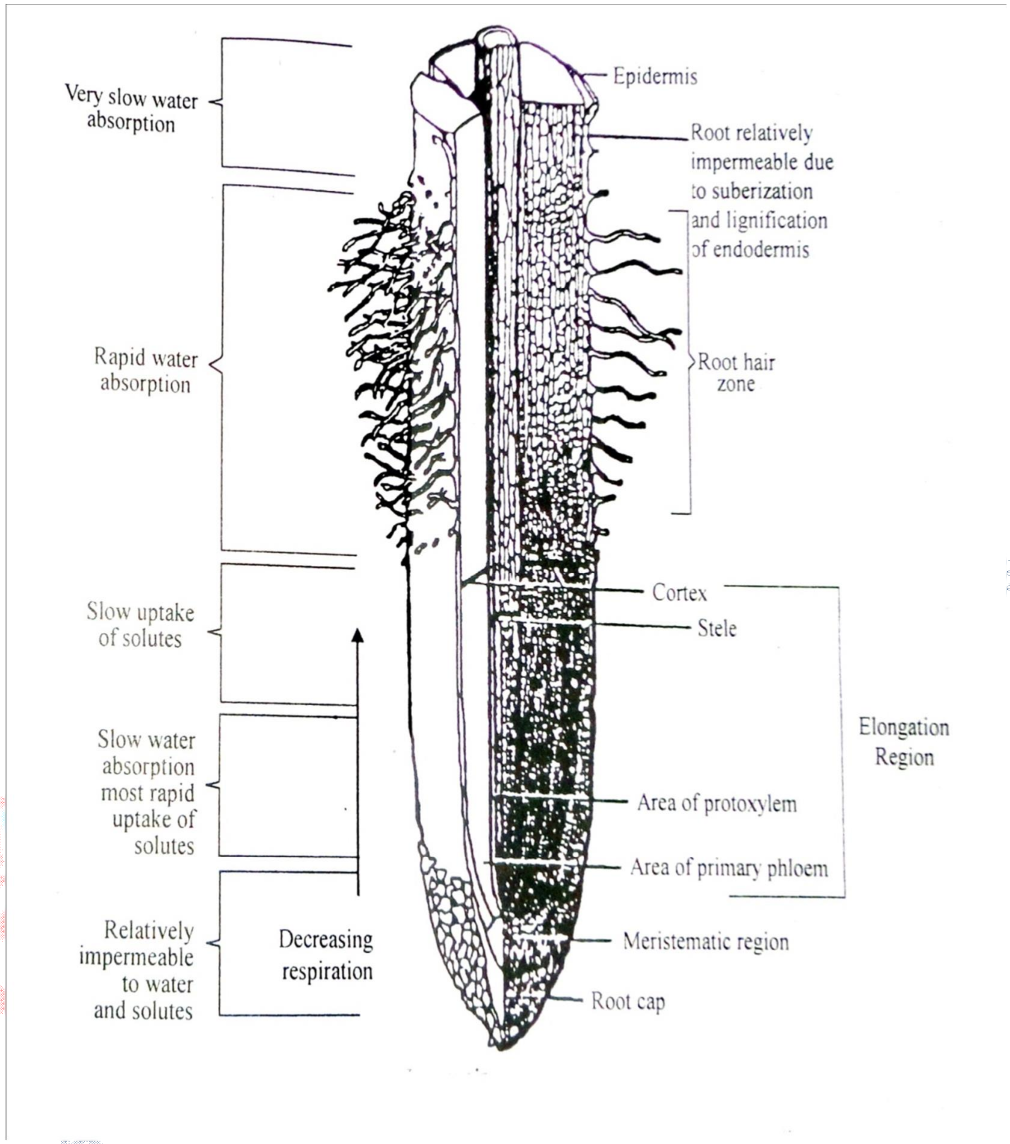


Fig. 10. Root apex regions and their functions

4.2 Types of Root Apex

Root apex has been classified into following five types on the basis of the method of origin of root cap and interrelations among histogens and primary tissues (Fig. 11):

(a) **First type:** In this type of root apex, a single solitary cell is found on the terminal position. This terminal cell produces root cap and other tissues of roots. This type of root apex is found in vascular cryptogams i.e. pteridophytes. Schuepp (1926) recognized this type as Type-A.

(b) **Second Type:** In such type of root apex, single layer of meristematic tissue is found. Epidermis, cortex, vascular tissues and root cap cells develop by this type of root apex. Such type of root apex organization is found in the members of Ranunculaceae and Amentiferae and monocotyledons. This type of root apex is also called as *Ranunculus* Type in dicots (and *Allium* Type when found in monocotyledons).

(c) **Third Type:** In most of the gymnosperms, two groups of initial cells are present in the root apex. The inner portion produces plerome while the outer portion produces periblem and root apex. Such type of root apex organization is seen in proteaceae and casuarinaceae. This type of root apex is also called as *Casuarina* Type in dicots and *Haemanthus* Type in monocots.

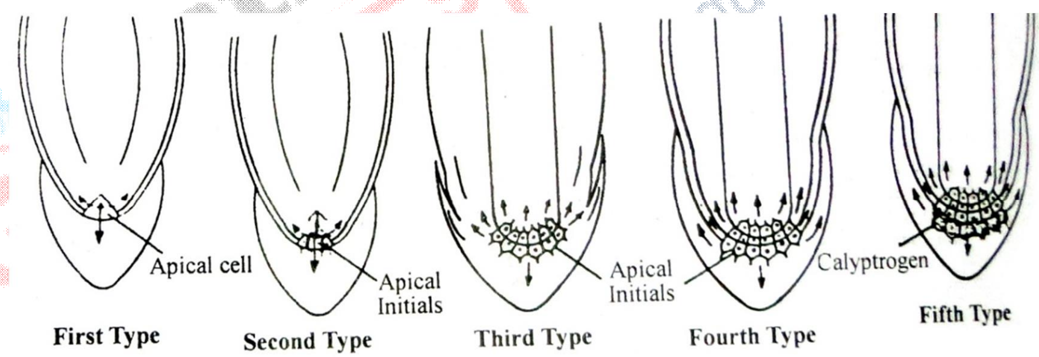


Fig.11. Various types of root apices

(d) **Fourth Type:** This type of root apex organization is found in the rest of angiosperms. In such type of root apices, meristematic cells are organized in three layers. The uppermost layer gives rise to dermatogen and root cap, middle layer gives rise to periblem and the inner region gives rise to plerome. In this type of root apex, root cap and epidermis are originated from the same single layered initial cells called as dermatocalyptrogen. Since, such type of root apex is commonly found in dicots, hence also called as Common Dicot Type, but when found in monocots, are called as *Zephryanthes* Type.

(e) **Fifth type:** Such type of root apex is found in monocots. In such of root apex, there are 5 layers of meristematic cells. The outer most layer gives rise to root cap, called as calyptrogen. The following layer of meristematic cells forms epidermis, i.e. dermatogen. Third and fourth layers give rise to periblem and plerome, respectively. This type of root apex organization is called as Maize Type or *Zea* Type.

4.3 Theories related to root apex organization

Multiple theories have been proposed to understand the structure and organization of root apex:

4.3.1 Apical Cell Theory:

This theory was proposed by Hofmeister (1957) and later elaborated by Nageli (1978). According to this theory, there is a tetrahedral cell in root apex which divides in three planes producing different tissues of roots. Division in the basal plane of this tetrahedral cell gives rise to root cap (Fig. 12).

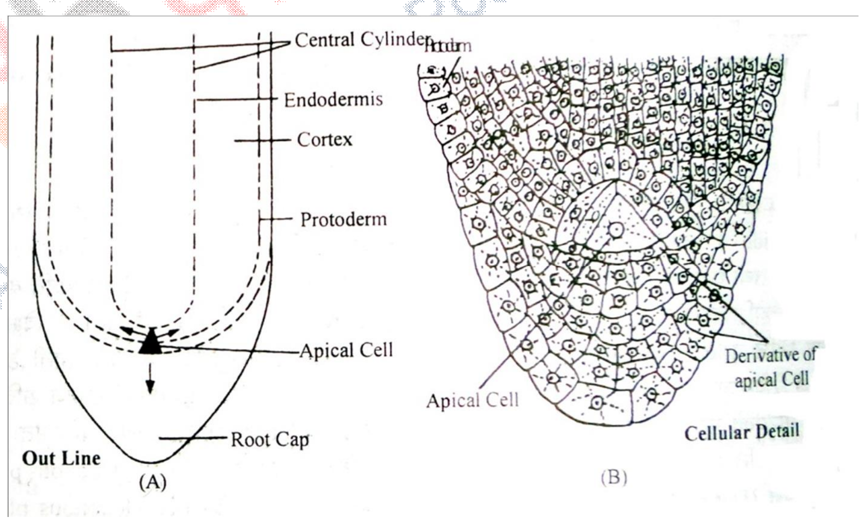


Fig. 12. LS of root apex of Ferns, outline (A), cellular details (b).

This theory is acceptable for some of the pteridophytes, e.g. polypodiaceae, Ophioglossaceae, Equisetaceae and Azollaceae because the differentiation and formation of various tissues and related regions in these plant groups becomes possible due to the activity of one apical cell. For example, according to Gunning et al. (1978) and Hardham (1979), the apical cell of root apex in *Azolla* divides for about 55 times to initiate root growth. However, this theory failed to explain the structure and organization of root apex in spermatophytes, i.e. gymnosperms and angiosperms, because there are group of meristematic initial cells in gymnosperms and angiosperms in the apical portion of the root apex which actively divide and differentiate to form different tissues of roots.

4.3.2 Histogen Theory:

Hanstein (1970) proposed this theory after studying the shoots and embryos of many angiosperms. He asserted that the meristematic cells of root apex are made of 3 layers exactly similar to shoot apical meristems. He identified the presence of 3 regions in shoots and roots (Fig. 13):

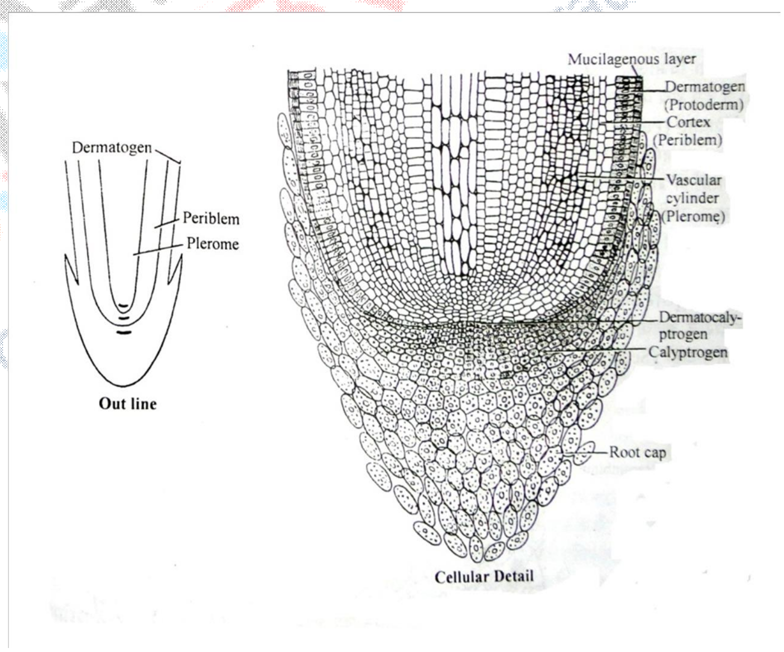


Fig. 13. LS of root apex depicting histogens.

(i) **Dermatogen**: This is the outermost layer of the cells of root apex and divide to form new cells. Later it produces tissues consisting smaller cells, called as calyptrogens. Calyptrogen is also a kind of meristematic cell and its activity makes root cap. Dermatogen produces epidermis.

(ii) **Periblem**: This region is just below the dermatogen layer. This region is apical most or middle portion of the root apex. This is single layered at apical portion but becomes multilayered in middle portion. Division and differentiation of this region gives rise to cortical region of the roots.

(iii) **Plerome**: Plerome is the central meristematic part of the apical meristem of the roots. This forms the stelar tissues, some parts of ground tissues like, pericycle, pith rays or medullary ray and pith.

These three layers were collectively called as histogen.

4.3.3 Korper-Kappe Theory:

This theory was proposed by Schuepp (1917). According to this theory, the cells of root apex are divided into two elements. The first division is of transverse type resulting into two cells, out of which one divides anticlinally, called as T-division. In some of the portions of the root apex, especially in the middle portion óTô is seen upright while in rest of the regions, inverted T is seen (⊥). When óTô is upright, then this is directed towards the apical portion, but, when óTô is inverted, it is directed opposite to the apical portion. Schuepp named upright óTô as Korper or body while inverted óTô was named as Kappy or cap. Such type of division is found in the members of poaceae. This theory is equivalent to the Tunica-Corpus Theory of shoot apex (Fig. 14).

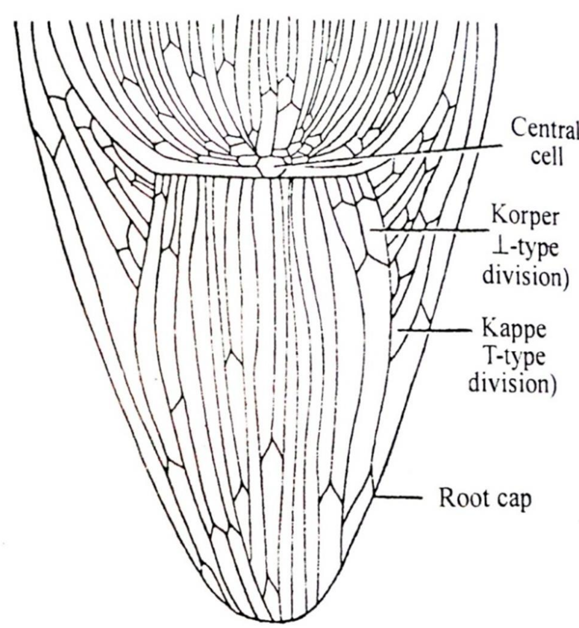


Fig. 14. LS of root apex depicting Korper-Kappe zones

4.3.4 Quiscent Centre Concept:

This concept was given by Clowes (1958). He studied root apex in *Zea mays* and ascertained the presence a cellular region in between root cap and meristematic cells called as Quiscent Centre (QC). The cells of QC remain inactive and often do not divide. Unlike the shoot apical meristems, the root apical meristems which flank the QC produce cells in two dimensions at its periphery and together produce most of the cells in an adult root. He recognized these cells as constituent of pro-meristem. At its terminus, the root meristem is covered by the root cap, which protects and guides its growth trajectory. Cells are continuously shed-off the outer surface of the root cap. Root apical meristem and tissue patterns are established at the very embryo stage in the case of the primary root (Fig. 15).

The cells of quiescent centre have lesser DNA, RNA and protein content. These cells have lesser number of ER and mitochondria. Nucleus and nucleolus are smaller in size. The QC cells are characterized by their low mitotic activity as they are maintained at the G1/S checkpoint in the cell cycles. Rate of DNA replication is lesser than those of other cells. QC acts as a reservoir of root cells to recover whatever is lost or damaged. The QC cells are pluripotent and are the source of stem cell initials.

The cells of quiescent centre remain inactive till the peripheral cells are in active stage of division, but start to divide in unfavorable condition, especially when roots are destroyed somehow and also when secondary roots are formed. They heal the wounds on secondary roots or damaged portion of the roots. Evidence suggests that the QC maintains the surrounding cells by preventing their differentiation via signals. The cells of QC actively divide when exposed to the damaging dose of X-ray while other meristematic cells do not show such responses. Histogen Theory and Korper-Kappe Theory successfully explain the organization of root apices except the presence of an independent calyptrogens and four-cell layered root in monocots. The activity of meristematic tissues enables roots to grow and the zone of elongation and root hair zone grow. Root cap protects the roots from the damage posed by positive geotropism. The cells of root cap are impermeable to water while meristematic cells of root apex have capability to absorb water along with their capacity to divide. The cells of zone of elongation do not efficiently absorb water while actively absorb the ions of mineral elements. The cells of root hair zone are most permeable for water. The cells of zone of maturation are lesser permeable due to the deposition of lignin and suberin.

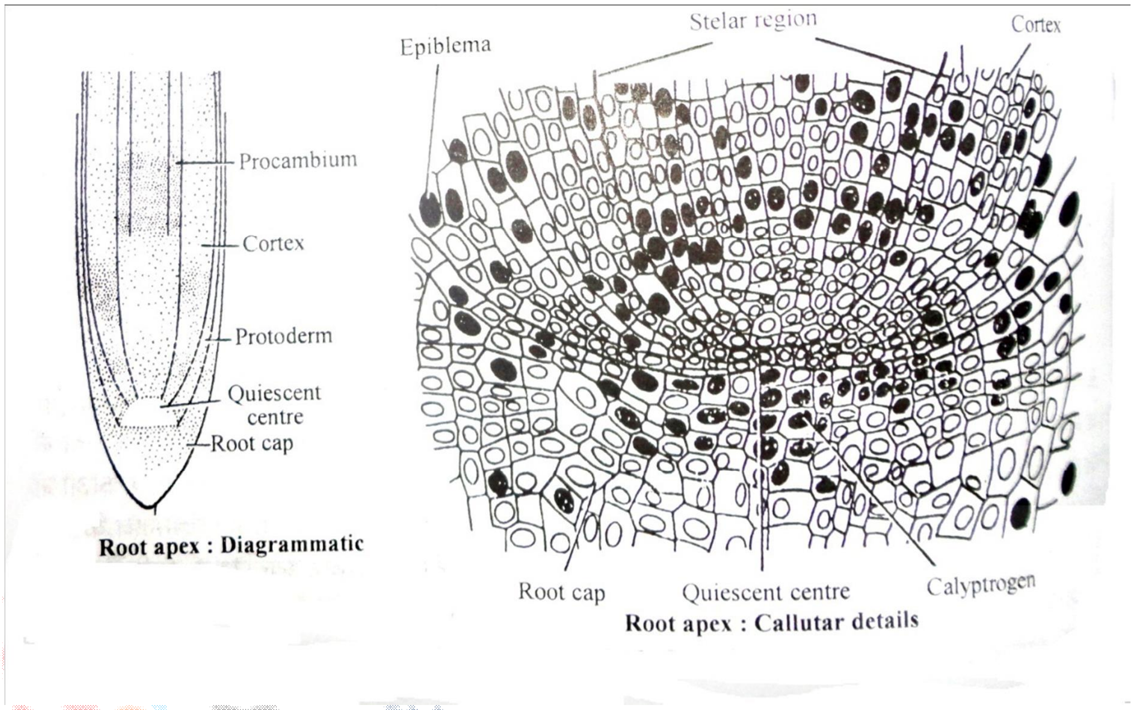


Fig. 15. Root apex (LS) showing Quiscent Centre, diagrammatic (A), cellular details (B)

5. **Floral meristem**

The shoot apical meristem may also transform into an inflorescence meristem i.e. floral meristem which produces sepals, petals, stamens and carpels of the flower. In contrast to vegetative apical meristems, floral meristems are responsible for determinate growth of the flower to a particular size and shape. The transition from shoot meristem to floral meristem requires floral meristem identity genes which specify the floral organs and terminate the production of stem cells.

6. Maintenance of un-differentiated states

Regulation of meristems through the cross-talk of phytohormones and genes

Maintenance of un-differentiated state of SAM and RAM is necessary for a perpetual growing plant. The growth of plants depends on the continuous function of meristems where a balance between the cell proliferation and differentiation is properly coordinated. Experiments on different mutants have shown that SAM is either to promote proliferation (i.e. promote the meristematic state) or to inhibit differentiation. The balance between the activity of the proliferation promoting (differentiation inhibiting) and the proliferation inhibiting (differentiation promoting) pathways is required for the long-term function of the SAM. It has also been found that these are independent pathways because each still functions in the absence of the other. Cell division and differentiation process in shoot and root apical meristems including the QC are strongly regulated by the interaction of number of phytohormones and genes. They act cooperatively, synergistically or antagonistically. The actively dividing and differentiating cells of the apical meristems also use cell-cell interactions as guides during the positional cues. These positional cues result in the activation some genes and inactivation of other genes by encoding a family of transcription factors in a set of events, thus successfully commencing their specific differentiation pattern based on their spatial location in the plant. Several genes have been identified that regulate this balance. Plant hormones are important factors involved in the balance between cell division and differentiation so that plant growth and development are tightly controlled in space and time. Division and differentiation are controlled by interactions between different phytohormones. Phytohormones include auxin (IAA), cytokinin (CK), gibberellins (GA), ethylene, abscisic acid (ABA), brassinosteroids (BRs). There are possibilities that non-hormonal factors may also interact with plant hormones through cell-cell communication.

IAA and CK are important for proper root and shoot development. IAA and CK have an antagonistic functional relationship in regulating size of the meristems. CK stimulates cell differentiation by suppressing auxin signalling and transport, while IAA promotes cell division by inactivating cytokinin signaling of shoot meristems. CK stimulates the differentiation in the root proximal meristem which leads to a decrease in the meristem size and growth. Thus, CK acts as an antagonistic counterpart of the cell division signals of IAA.

In the laboratory, if a set of undifferentiated meristem cells (callus) are grown in culture, they will not develop into a plant embryo unless they are stimulated with CK and IAA. A high ratio of CK/IAA will stimulate the meristematic cells to develop stems, leaves, and flower buds. On the other hand, a high IAA/CK ratio will stimulate the meristematic cells to develop roots. It has also been reported that polar IAA transport is regulated by phloem-transported, symplastic CK transport and that it maintains the vascular pattern of the root meristem.

GA controls cell proliferation in the shoot and root apical meristems and makes the plant taller and deep rooted in coordination with IAA. Ethylene up-regulates auxin biosynthesis and modulates transport-dependent auxin distribution, thereby inhibiting the expansion of cells in roots. ABA inhibits root growth at micromolar concentration, but stimulates it at a lower concentration. ABA also reduces the cell differentiation rate, resulting in an increase in the number of cells in the cell division zone and in the transition zone. BRs regulate root growth in a concentration-dependent manner. They inhibit root growth at high concentrations and promote it at lower concentrations. It has been found that BRs have a regulatory role in the control of cell-cycle and differentiation in *Arabidopsis* root meristem.

QC cells act as coordinator for many processes and events required for root meristem establishment and maintenance. When the asymmetrical division of a initial cell occurs, the resulting daughter cell which has contact with the QC remains as an initial cell, while another daughter cell apart from the QC remains dividing. QC cells may send short-range non-cell-autonomous signals which help the initials to remain in an undifferentiated state. Auxin regulates the maintenance of the QC and the activity of the root meristem. Auxin is synthesized at the shoot tip and is transported down to the QC. In addition, local biosynthesis of auxin in the root also takes place. Auxin determines the position of the QC and initial cells in the developing root. Auxin specifies the QC, regulates root meristem formation, and is a positional cue for the QC and initial cells. Ethylene also promotes cell division in the QC. The effect of auxin on the QC depends on auxin dependent ethylene biosynthesis for the QC. Ethylene also regulates statolith formation, which is a unique characteristic of the gravity-sensing columella cell in maize. In this regard, it was proposed that the communication between the root cap and QC and the resulting alteration in auxin distribution are the main controlling factors for the regulation of root cap size. ABA promotes QC maintenance and suppresses stem cell differentiation.

Redox status of the root tip maintains the undifferentiated state of RAM. Rduced glutathione/oxidized glutathione (GSH/GSSH) and reduced ascorbate/ dehydroascorbate (AsA/DHA) are important redox-regulating couples for maintaining the QC at the root tip. The QC is in a more oxidized state than the fast-dividing neighboring cells because the QC has lower levels of GSH and AsA than its surrounding cells. Ascorbate oxidase catalyzes the oxidation of AsA to DHA. Activity of the cell division at the QC could be established by the mutual control between auxin and the ascorbate oxidase level. In addition to the redox status and/or reactive oxygen species (ROS) in the RAM, reactive nitrogen species (RNS) such as nitrogen oxide (NO) also regulates primary root growth and auxin transport. An increase in the endogenous level of NO stimulated cell differentiation.