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):

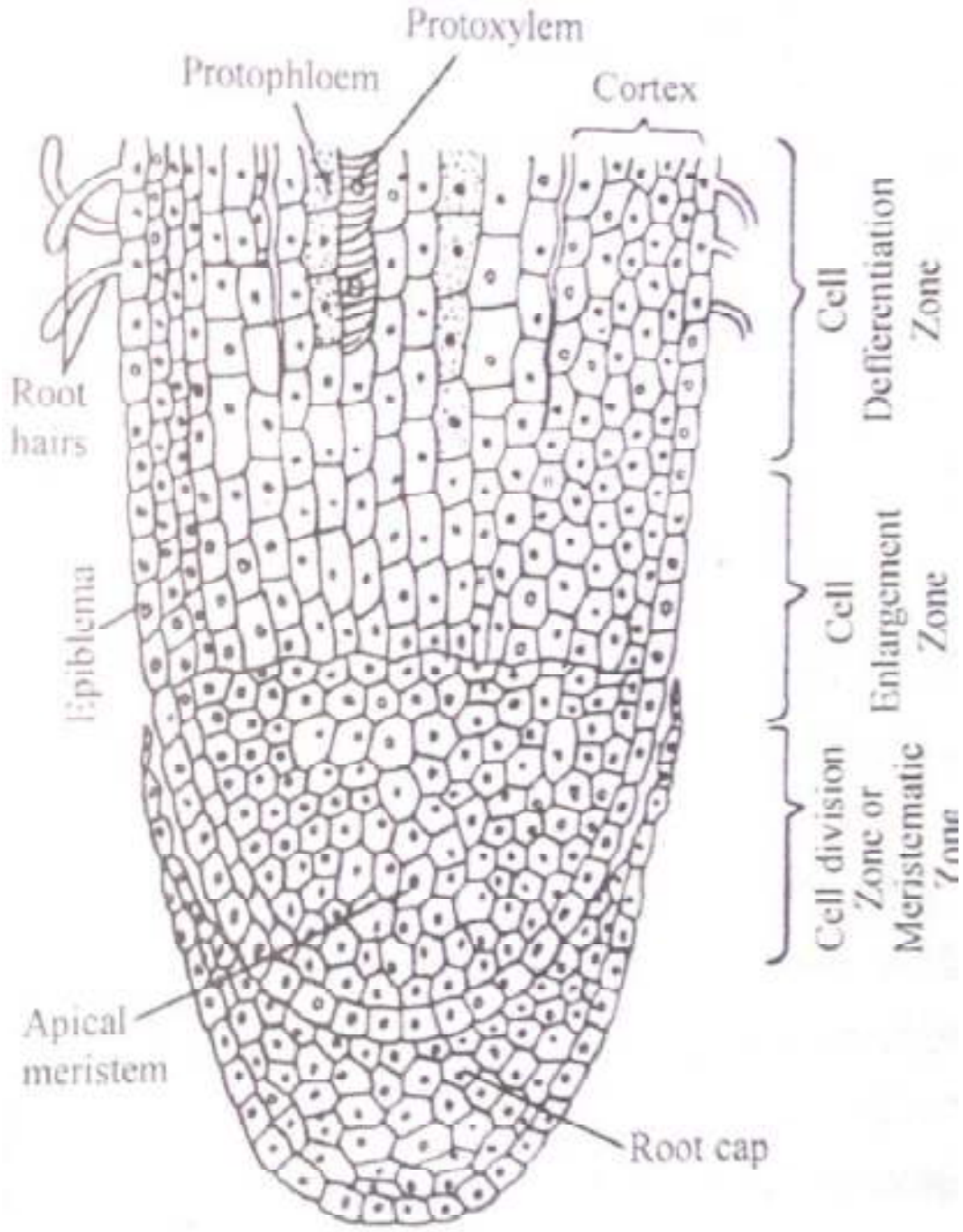

Fig. 9. LS of root apex.

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.

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).

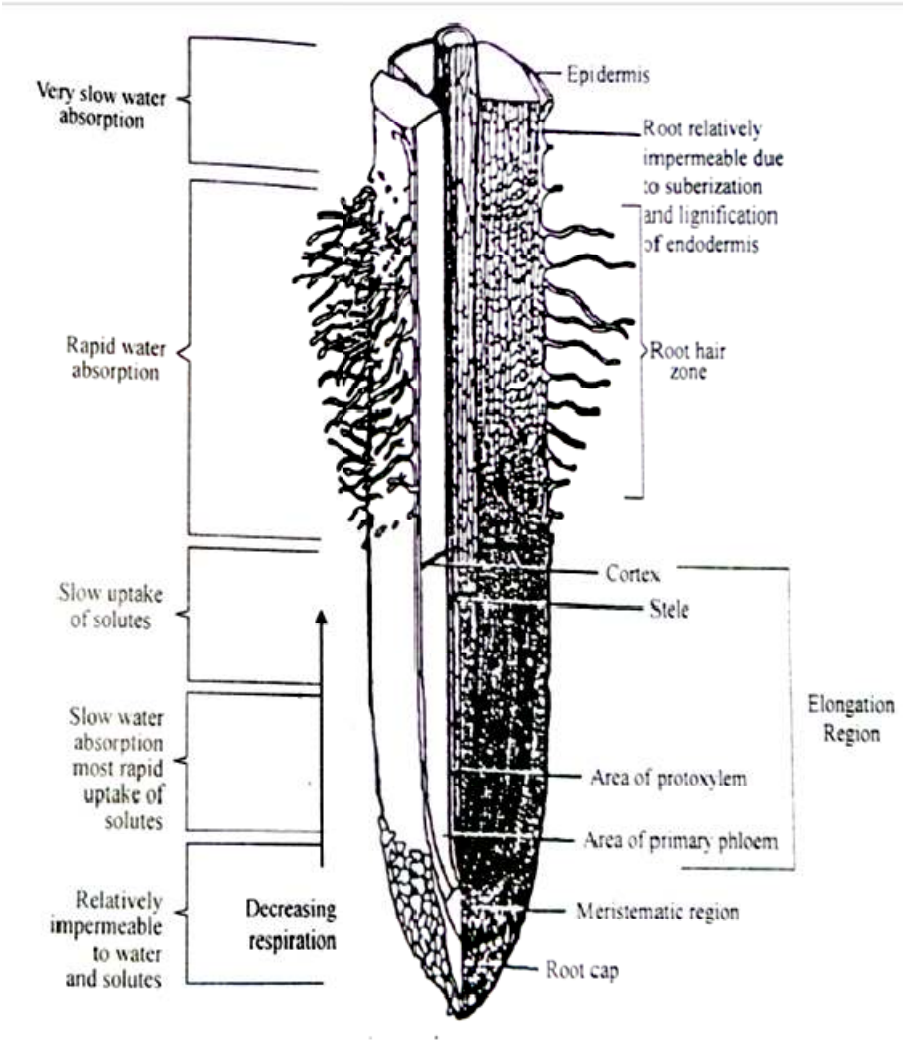

Fig. 10. Root apex regions and their functions

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.

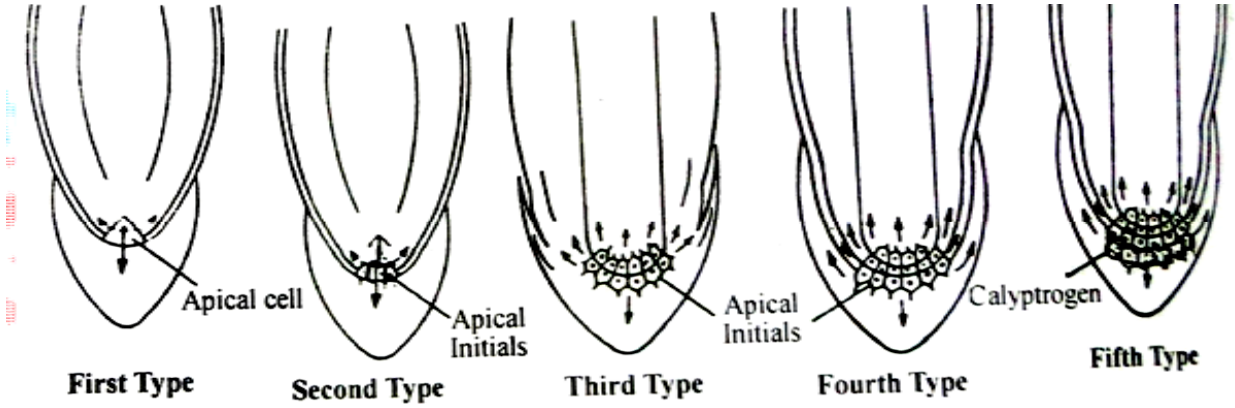

Fig.11. Various types of root apices

(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).

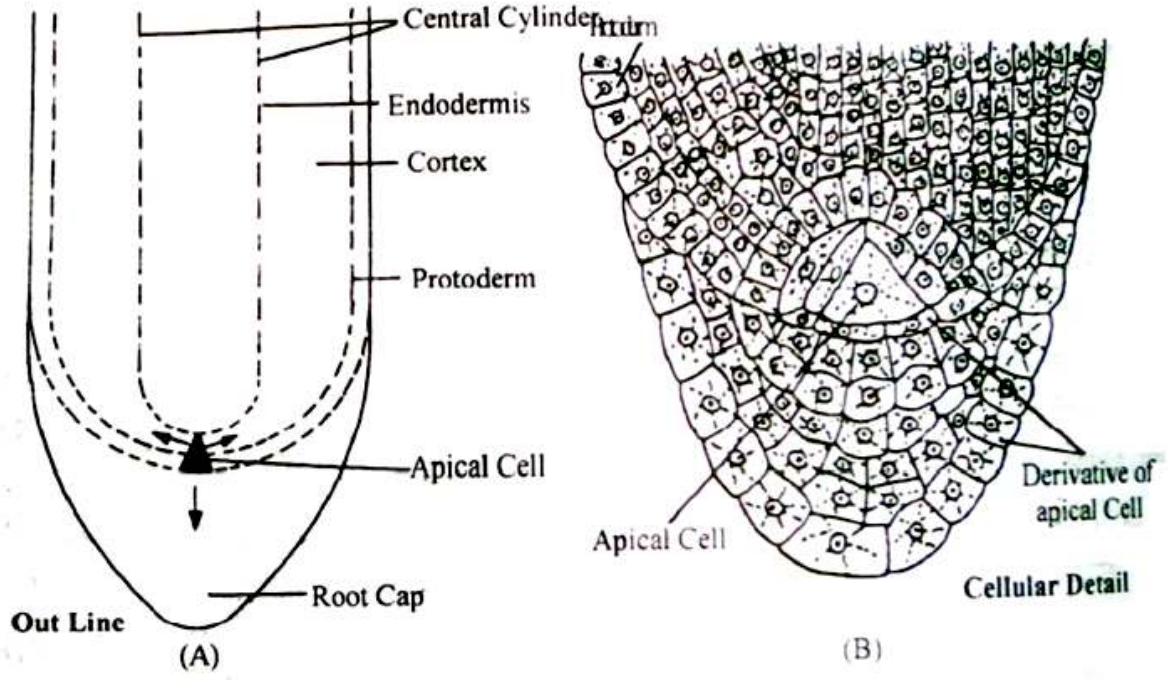

Fig. 12. LS of root apex of Ferns, outline (A), cellular details (b).

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):

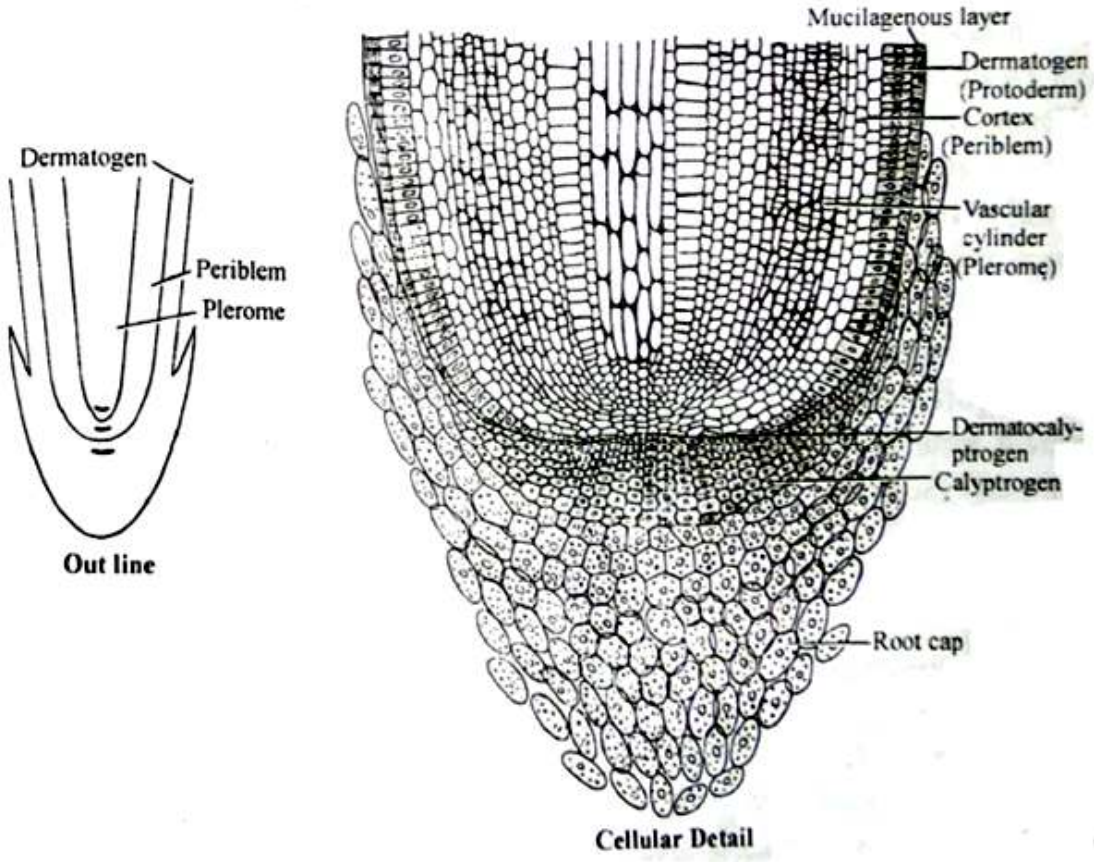

Fig. 13. LS of root apex depicting histogens.

(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 Tdivision. In some of the portions of the root apex, especially in the middle portion 'T' is seen upright while in rest of the regions, inverted T is seen (⊥). When 'T' is upright, then this is directed towards the apical portion, but, when 'T' is inverted, it is directed opposite to the apical portion. Schuepp named upright 'T' as Korper or body while inverted 'T' 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).

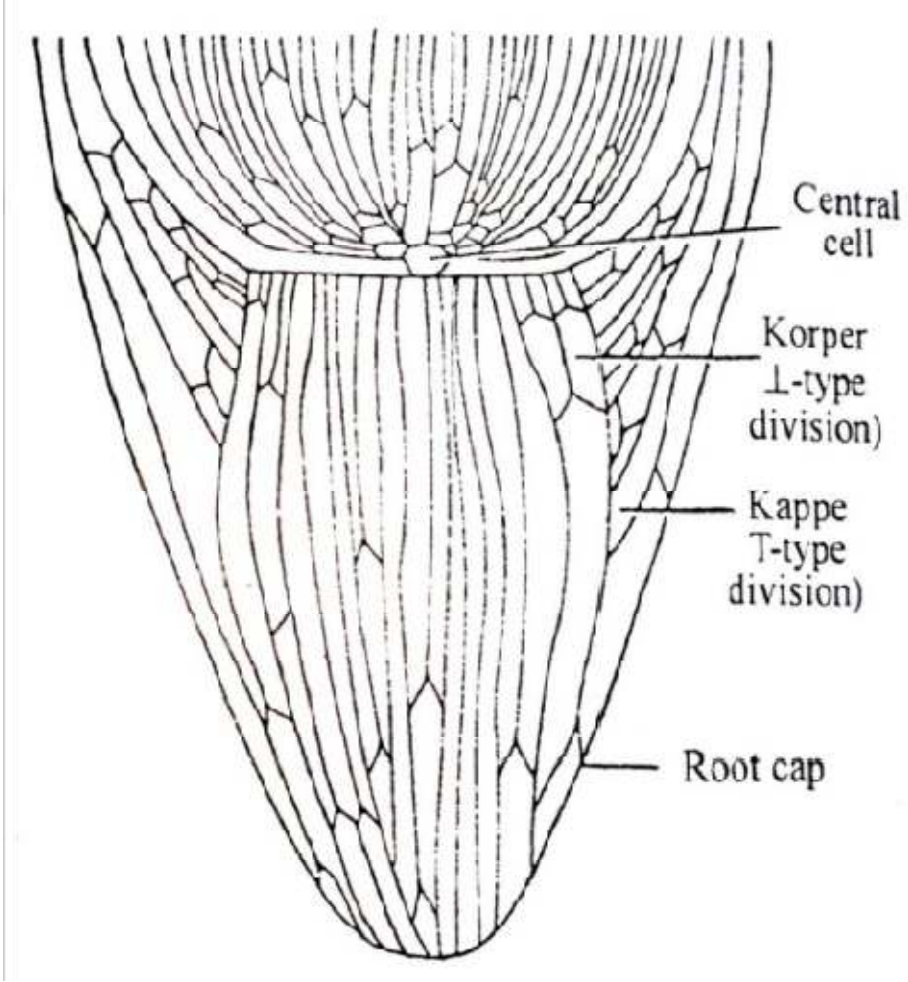

Fig. 14. LS of root apex depicting Korper-Kappe zones

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.

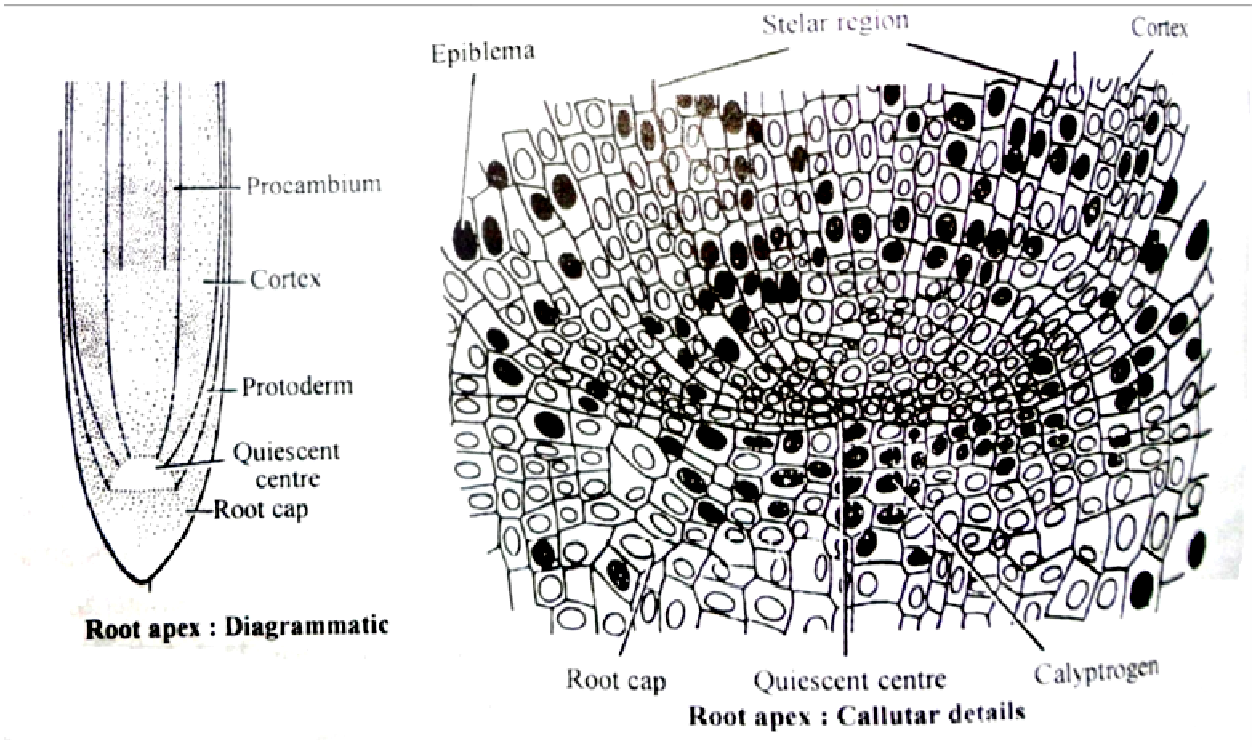

Fig. 15. Root apex (LS) showing Quiscent Centre, diagrammatic (A), cellular details (B).