Top 3 Theories of Root Apical Meristem in Plants

The following points highlight the top three theories of root apical meristem in plants. The theories are: 1. Apical Cell Theory 2. Histogen Theory 3. Korper-Kappe Theory.

1. Apical Cell Theory:
This theory was proposed by Nageli who drew the attention to the occurrence of a single apical cell or apical initial that composes the root meristem. A single apical cell is present only in vascular cryptogams, e.g. Equisetum, Adiantum and Polypodium etc. The apical initial is tetrahedral in shape and generates root cap from one side.

The other three sides donate cells to form epidermis, cortex and vascular cylinder. In other words all tissues that compose a mature root including root cap are the derivatives of a single apical cell. Apical cell theory is confined to vascular cryptogams only as the root apical meristem of flowering plants does not have a single apical cell.

2. Histogen Theory:

Hanstein in 1868 advocated the theory. According to Hanstein root apical meristem consists of three cell-initiating regions called histogens (Fig. 7.22). The histogens are called dermatogen, periblem and plerome that respectfully form epidermis, cortex and vascular cylinder that are present in a mature root.

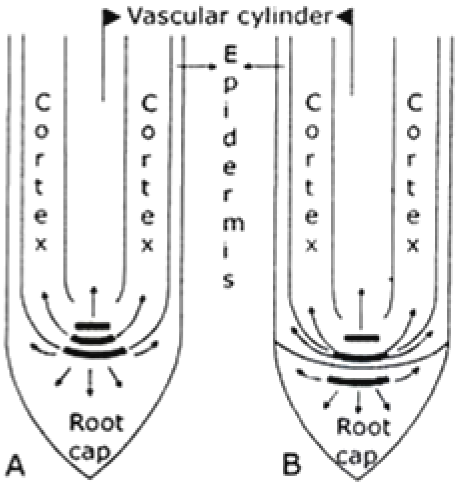


Figure 7.22

Schematic diagram of root apex based on Histogen theory. A. Root apex of *Raphanus sativa*. B. Root apex of *Zea mays* where root cap has its own histogen, i.e. Calyptrogen. Broad lines indicate histogens. Arrows indicate the direction of cell formation.

The derivatives of dermatogen vary. In Zea mays (monocot) dermatogen generates root cap only and this histogen is referred to as calyptrogen. In Brassica (dicot) dermatogen generates both protoderm and root cap and this histogen is referred to as dermatocalyptrogen.

Histogen theory explains both root and shoot apical meristem. This theory attributes specific destinies to the derivatives of the three histogens. Though histogen theory is abandoned to explain shoot apex, Eames and MacDaniels illustrated the root apical meristem on the basis of histogen concept.

3. Korper-Kappe Theory:

This theory of root meristem was proposed in 1917 by Schiiepp who regarded the occurrence of two systems of cell seriation that characterize the root apex with reference to planes of cell division in its parts.

Korper-kappe concept is also referred to as body-cap concept (Korper = body and kappe = cap) and the concept illustrates distinct type of cell wall pattern formation during cell division. The body-cap concept is illustrated below on analyzing the divisions in the derivatives of apical cell (Fig. 7.23).

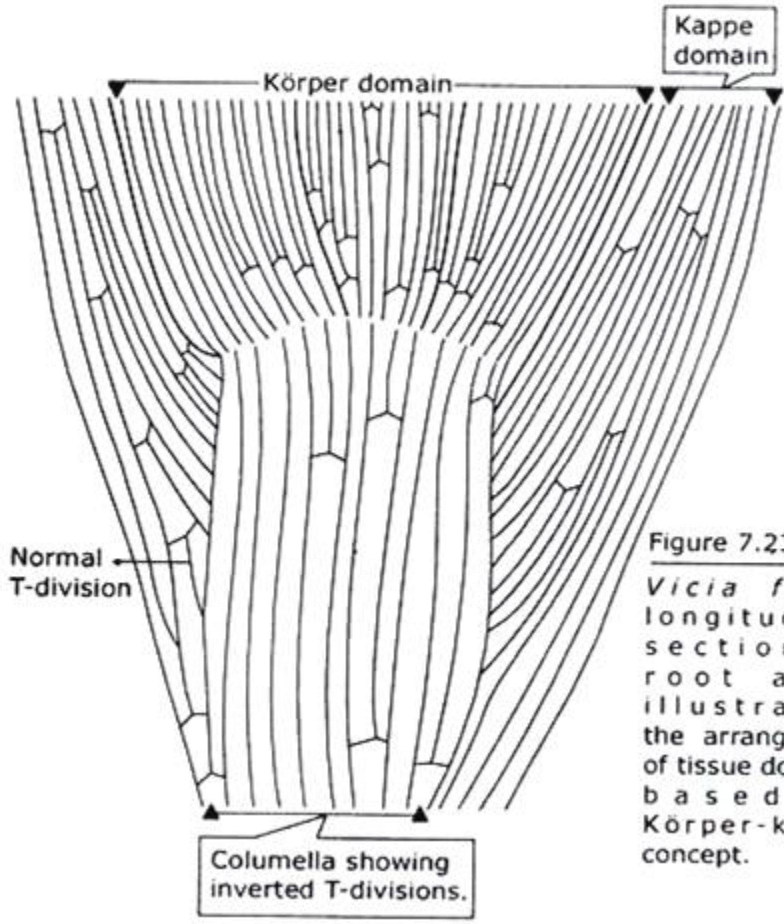


Figure 7.23

Vicia faba: longitudinal section of root apex illustrating the arrangement of tissue domains based on Körper-kappe concept.

The root meristem exhibits multicellular structure. It consists of conspicuous longitudinal files of cells. During growth the root changes in diameter. This happens due to cell divisions that occur in such a way that a single longitudinal file of cells becomes double files. The initial cell divides transversely. The two cells thus formed one has the capability of cell division. This cell divides longitudinally and both the daughter cells inherit the property of cell division.

The daughter cells are parallel in arrangement, share a common wall and divide by transverse partition followed by longitudinal partition in one cell. The sequences of wall formation when viewed together appear to form a configuration resembling the letter ‘T’ or ‘Y’. Such divisions are described as T-divisions. Continuous T-divisions result in the formation of double-rowed region over a single rowed region.

It is the T-division that characterizes korper and kappe. In the kappe the initial cell first divides transversely and forms two cells. The daughter cell that faces the root apex inherits the initial function. It divides longitudinally. The two cells thus formed have the capability of cell division.

When transverse and longitudinal partition are viewed together the combined cell walls appear as ‘T’ that is right-way-up. When such division continues it is observed that a single rowed region is left behind over the double-rowed region. This occurs in downwardly pointed roots.

In the korper the initial cell first divides by transverse partition and forms two cells. The daughter cell that faces the base of root, i.e. away from the apex inherits the initial function.

It divides longitudinally and the two daughter cells thus formed have the potentiality of cell division. The daughter cells divide by transverse partitions followed by longitudinal partitions. When transverse and longitudinal partitions are viewed together the cell walls form a configuration resembling an inverted ‘T’.

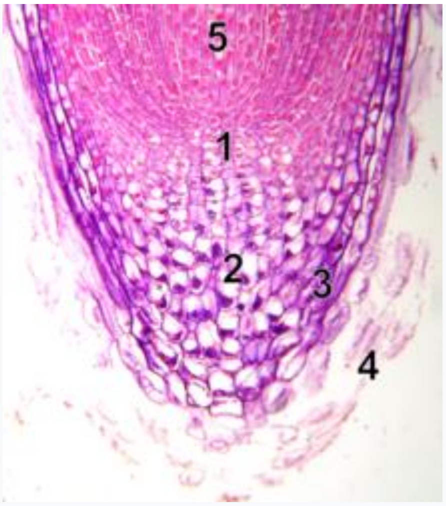
Korper and kappe-these two zones of root are delimited by planes of cell division. The zones exhibit clear boundary when they originate from separate initials, e.g. root with calyptrogen. The zones do not exhibit sharp demarcation line when they are the derivatives of same apical cell. In root with dermatocalyptrogen the cap extends into protoderm.

The central part of root cap is the columella where the cells are arranged in longitudinal files. These cells seldom divide. When division occurs the partition walls form the configuration of an inverted ‘T’ that is observed in the korper. The ‘T’ has normal configuration in the peripheral region of root cap.

The korper-kappe theory of root apex is comparable with tunica-corpus theory of shoot apex. The body-cap concept and tunica-corpus

> concept both are based solely on the planes of cell division. Anticlinal division is the characteristic of tunica whereas corpus exhibits both anticlinal and periclinal division.
>
> On the other hand the inverted ‘T’ – and normal ‘T’ pattern of cell wall formation are the characteristic of korper and kappe respectively. The boundaries between korper and kappe, and between tunica and corpus are not always sharply demarcated.

Root apical meristem[edit]



10x microscope image of root tip with meristem

1 - quiescent center

2 - calyptrogen (live rootcap cells)

3 - rootcap

4 - sloughed off dead rootcap cells

5 - procambium

Unlike the shoot apical meristem, the root apical meristem produces cells in two dimensions. It harbors two pools of stem cells around an organizing center called the quiescent center (QC) cells and together produces most of the cells in an adult root.[17][18] At its apex, the root meristem is covered by the root cap, which protects and guides its growth trajectory. Cells are continuously sloughed off the outer surface of the root cap. The QC cells are characterized by their low mitotic activity. Evidence suggests that the QC maintains the surrounding stem cells by preventing their differentiation, via signal(s) that are yet to be discovered. This allows a constant supply of new cells in the meristem required for continuous root growth. Recent findings indicate that QC can also act as a reservoir of stem cells to replenish whatever is lost or damaged.[19] Root apical meristem and tissue patterns become established in the embryo in the case of the primary root, and in the new lateral root primordium in the case of secondary roots.

Intercalary meristem[edit]

In angiosperms, intercalary meristems occur only in monocot (in particular, grass) stems at the base of nodes and leaf blades. Horsetails also exhibit intercalary growth. Intercalary meristems are capable of cell division, and they allow for rapid growth and regrowth of many monocots. Intercalary meristems at the nodes of bamboo allow for rapid stem elongation, while those at the base of most grass leaf blades allow damaged leaves to rapidly regrow. This leaf regrowth in grasses evolved in response to damage by grazing herbivores.

Floral meristem[edit]

When plants begin flowering, the shoot apical meristem is transformed into an inflorescence meristem, which goes on to produce the floral meristem, which produces the sepals, petals, stamens, and carpels of the flower.

In contrast to vegetative apical meristems and some efflorescence meristems, floral meristems cannot continue to grow indefinitely. Their future growth is limited to the flower with a particular size and form. The transition from shoot meristem to floral meristem requires floral meristem identity genes, that both specify the floral organs and cause the termination of the production of stem cells. *AGAMOUS* (*AG*) is a floral homeotic gene required for floral meristem termination and necessary for proper development of the stamens and carpels.[2] *AG* is necessary to prevent the conversion of floral meristems to inflorescence shoot meristems, but is identity gene *LEAFY* (*LFY*) and *WUS* and is restricted to the centre of the floral meristem or the inner two whorls.[20] This way floral identity and region specificity is achieved. WUS activates AG by binding to a consensus sequence in the AG’s second intron and LFY binds to adjacent recognition sites.[20] Once AG is activated it represses expression of WUS leading to the termination of the meristem.[20]

Through the years, scientists have manipulated floral meristems for economic reasons. An example is the mutant tobacco plant "Maryland Mammoth." In 1936, the department of agriculture of Switzerland performed several scientific tests with this plant. "Maryland Mammoth" is peculiar in that it grows much faster than other tobacco plants.

Apical dominance[edit]

Apical dominance is the phenomenon where one meristem prevents or inhibits the growth of other meristems. As a result, the plant will have one clearly defined main trunk. For example, in trees, the tip of the main trunk bears the dominant shoot meristem. Therefore, 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. The branch will start growing faster and the new growth will be vertical. Over the years, the branch may begin to look more and more like an extension of the main trunk. Often several branches will exhibit this behavior after the removal of apical meristem, leading to a bushy growth.

The mechanism of apical dominance is based on auxins, types of plant growth regulators. These are produced in the apical meristem and transported towards the roots in the cambium. If apical dominance is complete, they prevent any branches from forming as long as the apical meristem is active. If the dominance is incomplete, side branches will develop.[*citation needed*]

Recent investigations into apical dominance and the control of branching have revealed a new plant hormone family termed strigolactones. These compounds were previously known to be involved in seed germination and communication with mycorrhizal fungi and are now shown to be involved in inhibition of branching.[21]

Diversity in meristem architectures[edit]

The SAM contains a population of stem cells that also produce the lateral meristems while the stem elongates. It turns out that the mechanism of regulation of the stem cell number might be evolutionarily conserved. The *CLAVATA* gene *CLV2* responsible for maintaining the stem cell population in *Arabidopsis thaliana* is very closely related to the Maize gene *FASCIATED EAR 2*(*FEA2*) also involved in the same function.[22] Similarly, in Rice, the *FON1-FON2* system seems to bear a close relationship with the CLV signaling system in *Arabidopsis thaliana*.[23] These studies suggest that the regulation of stem cell number, identity and differentiation might be an evolutionarily conserved mechanism in monocots, if not in angiosperms. Rice also contains another genetic system distinct from *FON1-FON2*, that is involved in regulating stem cell number.[23] This example underlines the innovation that goes about in the living world all the time.

Role of the KNOX-family genes[edit]

Note the long spur of the above flower. Spurs attract pollinators and confer pollinator specificity. *(Flower: Linaria dalmatica)*

Complex leaves of *Cardamine hirsuta* result from KNOX gene expression

Genetic screens have identified genes belonging to the KNOX family in this function. These genes essentially maintain the stem cells in an undifferentiated state. The KNOX family has undergone quite a bit of evolutionary diversification while keeping the overall mechanism more or less similar. Members of the KNOX family have been found in plants as diverse as Arabidopsis thaliana, rice, barley and tomato. KNOX-like genes are also present in some algae, mosses, ferns and gymnosperms. Misexpression of these genes leads to the formation of interesting morphological features. For example, among members of *Antirrhineae*, only the species of the genus Antirrhinum lack a structure called spur in the floral region. A spur is considered an evolutionary innovation because it defines pollinator specificity and attraction. Researchers carried out transposon mutagenesis in *Antirrhinum majus*, and saw that some insertions led to formation of spurs that were very similar to the other members of *Antirrhineae*,[24] indicating that the loss of spur in wild *Antirrhinum majus* populations could probably be an evolutionary innovation.

The KNOX family has also been implicated in leaf shape evolution *(See below for a more detailed discussion)*. One study looked at the pattern of KNOX gene expression in *A. thaliana*, that has simple leaves and *Cardamine hirsuta*, a plant having complex leaves. In *A. thaliana*, the KNOX genes are completely turned off in leaves, but in *C.hirsuta*, the expression continued, generating complex leaves.[25] Also, it has been proposed that the mechanism of KNOX gene action is conserved across all vascular plants, because there is a tight correlation between KNOX expression and a complex leaf morphology.[26]

Primary meristems[edit]

Apical meristems may differentiate into three kinds of primary meristem:

- **Protoderm**: lies around the outside of the stem and develops into the epidermis.

- **Procambium**: lies just inside of the protoderm and develops into primary xylem and primary phloem. It also produces the vascular cambium, and cork cambium, secondary meristems. The cork cambium further differentiates into the phelloderm (to the inside) and the phellem, or cork (to the outside). All three of these 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.[27]
- **Ground meristem**: develops into the cortex and the pith. Composed of parenchyma, collenchyma and sclerenchyma cells.[27]

These meristems are responsible for primary growth, or an increase in length or height, which were discovered by scientist Joseph D. Carr of North Carolina in 1943.[*citation needed*]

Secondary meristems[edit]

There are two types of secondary meristems, these are also called the *lateral meristems* because they surround the established stem of a plant and cause it to grow laterally (i.e., larger in diameter).

- Vascular cambium, which produces secondary xylem and secondary phloem. This is a process that may continue throughout the life of the plant. This is what gives rise to wood in plants. Such plants are called arboraceous. This does not occur in plants that do not go through secondary growth (known as herbaceous plants).
- Cork cambium, which gives rise to the periderm, which replaces the epidermis.

Indeterminate growth of meristems[edit]

Further information: Root nodule

Though each plant grows according to a certain set of rules, each new root and shoot meristem can go on growing for as long as it is alive. In many plants, meristematic growth is potentially **indeterminate**, making the overall shape of the plant not determinate in advance. This is the **primary growth**. Primary growth leads to lengthening of the plant body and organ formation. All plant organs arise ultimately from cell divisions in the apical meristems, followed by cell expansion and differentiation. Primary growth gives rise to the apical part of many plants.

The growth of nitrogen-fixing root nodules on legume plants such as soybean and pea is either determinate or indeterminate. Thus, soybean (or bean and Lotus japonicus) produce determinate nodules (spherical), with a branched vascular system surrounding the central infected zone. Often, Rhizobium infected cells have only small vacuoles. In contrast, nodules on pea, clovers, and Medicago truncatula are indeterminate, to maintain (at least for some time) an active meristem that yields new cells for Rhizobium infection. Thus zones of maturity exist in the nodule. Infected cells usually possess a large vacuole. The plant vascular system is branched and peripheral.

Cloning[edit]

Under appropriate conditions, each shoot meristem can develop into a complete, new plant or clone. Such new plants can be grown from shoot cuttings that contain an apical meristem. Root apical meristems are not readily cloned, however. This cloning is called **asexual reproduction** or **vegetative reproduction** and is widely practiced in horticulture to mass-produce plants of a desirable genotype. This process is also known as mericloning.

Propagating through cuttings is another form of vegetative propagation that initiates root or shoot production from secondary meristematic cambial cells. This explains why basal 'wounding' of shoot-borne cuttings often aids root formation.[28]

Induced meristems[edit]

Meristems may also be induced in the roots of legumes such as soybean, *Lotus japonicus*, pea, and *Medicago truncatula* after infection with soil bacteria commonly called Rhizobia.[*citation needed*] Cells of the inner or outer cortex in the so-called "window of nodulation" just behind the developing root tip are induced to divide. The critical signal substance is the lipo-oligosaccharide Nod factor, decorated with side groups to allow specificity of interaction. The Nod factor receptor proteins NFR1 and NFR5 were cloned from several legumes including *Lotus japonicus*, *Medicago truncatula* and soybean (*Glycine max*). Regulation of nodule meristems utilizes long-distance regulation known as the autoregulation of nodulation (AON). This process involves a leaf-vascular tissue located LRR receptor kinases (LjHAR1, GmNARK and MtSUNN), CLE peptide signalling, and KAPP interaction, similar to that seen in the CLV1,2,3 system. LjKLAVIER also exhibits a nodule regulation phenotype though it is not yet known how this relates to the other AON receptor kinases.

(NOTE:-We have used the word " DIFFERENTIATION " for the process of dividing of tissues which makes them specific to particular shape, size, and function.)[*citation needed*]