ORGANIZATION OF SHOOT APICAL MERISTEM

6 LECTURES

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The only way to save a rhinoceros is to save the environment in which it lives, because there's a mutual dependency between it and millions of other species of both animals and plants.

- David Attenborough

Tissue is a cellular organisational level between cells and a complete organ. A tissue is an ensemble of similar cells and their extracellular matrix from the same origin that together carry out a specific function. Organs are then formed by the functional grouping together of multiple tissues.

Meristem is the tissue in plants containing undifferentiated cells (meristematic cells), found in zones of the plant where growth can take place. Meristematic cells give rise to various organs of a plant and are responsible for growth.

Differentiated\(^1\) plant cells generally cannot divide or produce cells of a different type. Meristematic cells are incompletely or not at all differentiated, and are capable

\(^1\) Cell differentiation is the process by which dividing cells change their functional or phenotypical type. All cells presumably derive from stem cells and obtain their functions as they mature. Dedifferentiation is a reverse epigenetic reprogramming resulting in the loss of phenotypic specialization and reversion of cells to a less differentiated state that allows them to proliferate and redifferentiate into their parent cell type.
of continued cellular division. Therefore, cell division in the meristem is required to provide new cells for expansion and differentiation of tissues and initiation of new organs, providing the basic structure of the plant body.

**Theories of Shoot Apical Meristem in Plants**

**Histogen Theory:**

Hanstein in 1868 put forward histogen theory (histogen means tissue builder). According to this theory the tissues of a plant body originate from a mass of meristem where the following three (histogens) can be distinguished:

(a) **Dermatogen**: It is the outermost layer of the meristem. It gives rise to epidermises of root and stem.

(b) **Periblem**: This region occurs internal to dermatogen but peripheral to plerome. This histogen is destined to form cortex of root and shoot and inner tissues of leaves. It surrounds plerome.

(c) **Plerome**: (In Greek meaning that this fills). This region gives rise to vascular cylinder of stem and root including pith. It is the central core of stem and root and the cells composing this zone are very irregular. This region is enveloped by a variable number of mantle-like layers which are represented by dermatogen and periblem.

According to Hanstein dermatogen, periblem and plerome arise from independent initials of the apical meristem.

Later investigations reveal that the sub-divisions — dermatogen, periblem and plerome have no universal application due to the following two reasons:

(i) In gymnosperm and angiosperm there exists no clear distinction between periblem and plerome.

(ii) The respective roles of the three histogens cannot be demonstrated.
The main weakness of Hanstein’s concept was to assign specific destinies of histogens. The histogens — dermatogen, periblem and plerome are committal and respectfully give rise to epidermis, cortex and stele. Later this theory was superseded by tunica-corpus theory because the zones are noncommittal.

The present-day concept is that the different zones in the shoot apex are fundamentally same and capable of producing all tissues. It is the position in the meristem that determines the destiny of derivatives. This is due to the fact that in zones some genes are activated and others are repressed resulting in the production of different tissues.
Tunica-Corpus Theory:

Schmidt in 1924 postulated tunica-corpus theory on the basis of studies of shoot apices of angiosperm. This theory is concerned with planes of cell division in the apex. **In contrast to apical cell theory and histogen theory tunica-corpus theory is applicable only to shoot apex and not to root.** Schmidt distinguishes two tissue zones in the shoot apex and termed them as tunica and corpus.

Majority of angiosperm shoot apex exhibits tunica consisting of two layers of cells and corpus (Fig. 7.9 A). Researchers designate the layers as L1, L2 and L3 to denote respectively outer layer of tunica, inner layer of tunica and corpus.

**Tunica-Corpus model of the apical meristem (growing tip).** The epidermal (L1) and subepidermal (L2) layers form the outer layers called the tunica. The inner L3 layer is called the corpus. Cells in the L1 and L2 layers divide in a sideways fashion, which keeps these layers distinct, whereas the L3 layer divides in a more random fashion.

**Tunica:**

Tunica is the peripheral tissue zone of shoot apex. It consists of one or more peripheral layers of cells. Dicotyledons exhibit one to five layers of cells in tunica; two layers of cells are represented by largest number of species. Monocotyledons have one to four layers of cells in tunica; one and two layered tunica predominates in it. One single layered tunica is termed as **monostatose.** Many layered tunica is termed as **multistratose.** Xanthorrhoea media shows eighteen layered tunica.

Tunica is characterized in having **anticlinal** plane of cell division, i.e., the division wall is laid down perpendicular
to the surface. This division reflects to the surface growth in the apex. As a result **tunica grows as a sheet but not in thickness.**

Tunica cells undergoes **anticlinal** division, that is cell division perpendicular to the plant surface

The main function of tunica is to give rise epidermis. Sometimes the inner layers of tunica form cortex and vascular tissue.

[Cytochimera: Chimaera, also spelt as chimera, refers a plant or plant organ having tissues of varied genetic origin lying adjacent to one another. In some plant the meristematic region consists of at least two populations of cells that differ in their chromosome numbers. The chimera of this plant is recognizable only at the cytological level and termed as cytochimera.

Shoot apices are induced to form cytochimeras to study the function of L1, L2 and L3 layers. Treating the shoot apex with colchicine does this. The alkaloid colchicine, a chemical mutagen, is obtained from the plant Colchicum autumnale. Colchicine has the property to disrupt the spindle microtubules formed during mitosis. The drug colchicine is applied to the shoot tips by slow trickling or as paint.

The treatment temporarily blocks mitosis. The cells that are in metaphase stage cannot complete chromosome movement due to the failure of spindle mechanism but the other events of mitosis do continue. As a result nuclei are formed with tetraploid chromosome numbers. Then colchicine was washed out and the meristems were allowed to continue cell division.

Staining properties of nucleus can recognize the descendents of tetraploid cell. Using this technique it becomes possible to find that the LI layer, i.e. the outermost layer gives rise to the epidermis of a leaf and the inner layers donate cells to form mesophyll and vascular tissues.

In stems LI gives rise to epidermis and the rest forms the cortex and vascular tissue. In Datura the shoot apices were experimentally induced to develop cytochimera. The apices exhibited that the cells of LI, L2 and L3 layers had nuclei with chromosome number respectfully 8n, 2n and 2n; 4n, 2n and 4n, and 2n, 8n and 4n].

It is the anticlinal plane of cell division that characterizes tunica. In maize, certain grasses like Agropyron repens and Chlorogalum pomeridianum (Liliaceae) etc. periclinal divisions are observed in tunica. This led anatomists to modify the ‘strictness of definition of the tunica’. One view regards that the tunica should
include only those layer(s) that exhibit anticlinal plane of division. If any inner layer(s) of tunica show periclinal division they are to be assigned to corpus.

Other workers treat tunica in a very loose sense and regard that the inner layer(s) may divide periclinally. So to avoid discrepancies the term mantle was proposed in a loose sense instead of tunica. Corpus was replaced by the term core. Mantle overarches core. Popham and Chan (1950) advocated the mantle and core concept in the shoot apex and they did not take into account to the planes of cell division.

Cytologically two zones are recognized in the tunica though all cells exhibit the same anticlinal cell division. The first zone is central apical zone and the second occurs between the central apical zone and leaf primordium.

The central apical zone consists of one or few initial cells that are larger and contain large nuclei and vacuoles than the cells of the second zone. The cells of the second zone are small and more darkly staining than the cells of the first zone. In contrast to first zone periclinal division may occur in the second zone close to the leaf primordium in addition to anticlinal division.

Corpus:
Corpus is the inner-most bulky tissue zone of shoot apex. It consists of cells that are several cell layers deep. Tunica overarches corpus. Meristematic tissues composing this zone are larger than tunica. The cells of corpus are arranged haphazardly, as opposed a good the neat linear arrangement of tunica. The cells of corpus show both anticlinal and periclinal division.

Generally corpus is destined to give rise cortex and vascular tissue.

Usually corpus is not homogeneous. It consists of several zones. The corpus is composed of three zones:
(a) Central mother cells —the uppermost zone of corpus.
(b) Pith-rib meristem that occurs below the central mother cell zone.
(c) Flank meristem (also called peripheral meristem) m surrounds both central mother cell zone and pith-rib meristem. The peripheral zone is shaped like a truncated hollow cone.

The component cells of tunica and corpus differ in size, shape, plane of cell division and topography. Ultrastructurally each zone is composed of cells that have characteristic architectures as is revealed by quantitative techniques.

Merits of tunica-corpus theory:
1) It deals with one thing, i.e. planes of cell division. As a result the description of meristem becomes precise.
ii) It has topographical value in the studies of development of different tissue system in plants.

iii) The destiny of derivatives of corpus is not predetermined.

iv) The derivatives of the zones are not rigid like histogen theory.

v) It explains clearly the growth pattern in the shoot apex of angiosperm.

vi) It enables to understand the development of leaves as they arise close to apex.

vii) The specific variation in the number of tunica layers may be of taxonomic significance, e.g. grasses.

Tunica-corpus organization of shoot apical meristem is observed in angiosperm only. Cryptogams and majority of gymnosperm do not exhibit tunica-corpus organization. They do not have any stable surface layer that divides only by anticlinal division.

Araucaria and Ephedra have a single stable surface layer that divides only by anticlinal division.

Thus they exhibit tunica-corpus pattern. Tunica-corpus theory is noncommittal regarding the ultimate destiny of cell-lineages. In present-day concept all cells in the shoot apex with tunica-corpus organization are fundamentally same and have equal potentiality. In corpus the cells of peripheral zone and pith-rib meristem are also same as they owe their origin from central mother cell zone.

But during differentiation some genes are repressed and others are activated resulting in the production of different tissues. It is thought that if some how or means the cells of peripheral meristem zone of corpus is transferred to the location of pith-rib meristem, the cells will produce pith cells.

In conclusion it is to mention that tunica-corpus theory provides a flexible description of cell arrangement in the shoot apex and this is not rigid like histogen theory. It has served well in understanding the structure of shoot apical meristem and the origin and development of leaf.
The shoot apices of angiosperm exhibit cytohistological zonation in addition to tunica corpus zonation (Fig. 7.10). Four zones are recognized namely:

1. Tunica initials—consist of an apical group of cells,
2. Corpus initials—that occur below apical initials and are similar to central mother cells,
3. A peripheral zone and
4. A rib meristem.

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. Leaf primordia originate from this layer.

**Structure of root apical meristem**
The root cap protects the apical meristem from mechanical injury as the root pushes its way through the soil. Root cap cells form by specialized root cap stem cells. As the root cap stem cells produce new cells, older cells are progressively displaced toward the tip, where they are eventually sloughed off. As root cap cells differentiate, they acquire the ability to perceive gravitational stimuli and secrete mucopolysaccharides (slime) that help the root penetrate the soil.

- The meristematic zone lies just under the root cap, and in Arabidopsis it is about a quarter of a millimeter long. The root meristem generates only one organ, the primary root. It produces no lateral appendages.
- The elongation zone, as its name implies, is the site of rapid and extensive cell elongation. Although some cells may continue to divide while they elongate within this zone, the rate of division decreases progressively to zero with increasing distance from the meristem.
- The maturation zone is the region in which cells acquire their differentiated characteristics. Cells enter the maturation zone after division and elongation have ceased. Differentiation may begin much earlier, but cells do not achieve the mature state until they reach this zone. The radial pattern of differentiated tissues becomes obvious in the maturation zone. Later in the chapter we will examine the differentiation and maturation of one of these cell types, the tracheary element.

As discussed earlier, lateral or branch roots arise from the pericycle in mature regions of the root. Cell divisions in the pericycle establish secondary meristems that grow out through the cortex and epidermis, establishing a new growth axis (Figure 16.18). The primary and the secondary root meristems behave similarly in that divisions of the cells in the meristem give rise to progenitors of all the cells of the root.

Root Stem Cells Generate Longitudinal Files of Cells

Meristems are populations of dividing cells, but not all cells in the meristematic region divide at the same rate or with the same frequency. Typically, the central cells divide much more slowly than the surrounding cells. These rarely dividing cells are called the quiescent center of the root meristem (see Figure 16.17). Cells are more sensitive to ionizing radiation when they are dividing. This is the basis of the use of radiation as a treatment for cancer in humans. As a result, the rapidly dividing cells of the meristem can be killed by doses of radiation that nondividing and slowly dividing cells, such as those of the quiescent center, can survive. If the rapidly dividing cells of the root are killed by ionizing radiation, in many cases the root can regenerate from the cells of the quiescent center. This ability suggests that quiescent-center cells are important for the patterning involved in forming a root.

The Quiescent Centre is a group of cells, up to 1,000 in number, in the form of a hemisphere, with the flat face toward the root tip. It is a region in the apical meristem of a root where cell division proceeds very slowly or not at all, but the cells are capable of resuming meristematic activity should tissue surrounding them be damaged. Cells of root apical meristems do not all divide at the same rate.
FIGURE 4.3 Pathways for water uptake by the root. Through the cortex, water may travel via the apoplastic pathway, the transmembrane pathway, and the symplastic pathway. In the symplastic pathway, water flows between cells through the plasmodesmata without crossing the plasma membrane. In the transmembrane pathway, water moves across the plasma membranes, with a short visit to the cell wall space. At the endodermis, the apoplastic pathway is blocked by the Caspian strip.
The most striking structural feature of the root tip, when viewed in longitudinal section, is the presence of the long files of clonally related cells. Most cell divisions in the root tip are transverse, or anticlinal, with the plane of cytokinesis oriented at right angles to the axis of the root (such divisions tend to increase root length). There are relatively few periclinal divisions, in which the plane of division is parallel to the root axis (such divisions tend to increase root diameter).

**Ground tissue system/ simple tissues**

The ground tissue of plants includes all tissues that are neither dermal (AKA epidermis, is a single layer of cells that covers the leaves, flowers, roots and stems of plants. It forms a boundary between the plant and the external environment) nor vascular. It can be divided into three types based on the nature of the cell walls.

Ground tissues are produced by the ground meristems. This tissue type comprises the majority of the plant body. Ground tissue system includes three cell types of different functions: parenchyma, collenchyma and sclerenchyma.

**Parenchyma**
Parenchyma cells have thin primary walls and usually remain alive after they become mature. Parenchyma forms the "filler" tissue in the soft parts of plants. The meristematic cells are also parenchymatous in nature.

Parenchyma cells are slightly differentiated cells, still being capable of dividing. Among certain circumstances they can dedifferentiate into dividing tissues (secondary meristems). Out of these cells the whole plant may be regenerated; this process is called redifferentiation. Parenchyma cells are characterized by complete plasticity. They are large, usually isodiametrical cells. Nevertheless, lobed or branched parenchyma cells also occur in some plants. Large central vacuole is also a typical feature of the parenchyma cell, thus its cytoplasm forms a thin layer adjacent to the cell wall. Its cell wall is composed of cellulose, mostly without any other deposited material. Its secondary cell wall is typically pitted, which indicates plasmodesmal connections between the neighboring cells.

**Functional classification of parenchyma**

Assimilatory parenchyma or chlorenchyma: parenchyma, containing chloroplasts, adapted for photosynthesis. Most typically, it constitutes the mesophyll of the leaf, yet it is also present in any other green plant organs (e.g. stems, unripe fruits).

a. Storage parenchyma: this tissue type is characteristic of storage organs, so it occurs principally in roots, rhizomes, bulbs, tubers, seeds or cotyledons. The accumulated compound is chiefly starch. Sugars may also be stored as sucrose accumulated in the vacuole, as in the sugar beet. Proteins are stored in protein vacuoles; in seeds, they are present as solid aleurone grains. Lipids are accumulated in the elaioplasts or as lipid bodies in the cytoplasm.

b. Aerenchyma: The typical parenchyma of water plants and species living in moist habitats. It may occur in the root, stem and leaf as well. It has typically enlarged intercellular cavities, what is often due to the characteristically branched or lobed cell forms. It is of crucial importance for the oxygen supply and gas exchange of these plants.

c. Water storage parenchyma: The characteristic ground tissue of succulent plants living in arid habitats. This strategy of drought adaptation is achieved by storing the rare but periodically high precipitation either in the stem or in the leaves. Water is absorbed in the form of mucilage.

d. Secretory parenchyma: Plant secretion may occur both via external, epidermal structures (e.g. glandular trichomes) and within internal tissues. Internal secretion is served by specialized parenchyma cells, that sometimes observed individually or even in clusters. Secreted material gathers within internal cavities or secretory canals. The inner cavity may be formed lysigenously, that is the result of cell lysis (e.g. secretion of volatile oils in the pericarp of citrus species), or schizogenously, which means the separation of the cell walls along the middle lamella. In the latter case, the cavity is lined with epithelial cells (e.g. resin ducts of pines). Sometimes secretory cells are scattered among other cell
types. Often these cells also store the secreted material (e.g. tannin cells). Further characteristic secretory structures are the laticifers producing a fluid called latex. Laticifers may be articulated or nonarticulated.

Supporting or mechanical ground tissues (collenchyma & sclerenchyma)

Collenchyma

Collenchyma cells have thin primary walls with some areas of secondary thickening. Collenchyma provides extra mechanical and structural support, particularly in regions of new growth. They are elongated cells with irregular cell walls. The cells have thick deposits of cellulose in their cell walls and appear polygonal in cross section. The strength of the tissue results from these thickened cell walls and the longitudinal interlocking of the cells. Collenchyma may form cylinders or occur as discrete strands and is one of the three ground, or fundamental, tissues in plants, together with parenchyma (living thin-walled tissue) and sclerenchyma (dead support tissue with thick cell walls).

The collenchyma cells are living with vacuolate protoplast. Chloroplasts may also be present. Though normally collenchyma cells are narrower and longer than parenchyma, the two types of tissues very often intergrade; even transitional forms may occur. Like parenchyma it can undergo reversible changes and retain the capacity of cell division. On account of these similarities collenchyma is considered a type of parenchyma specially adapted for supporting function. The most distinctive character of the collenchyma cells is the cell wall which becomes unevenly thickened. There are different methods of deposition, but commonly, the thickenings are confined to the corners of the cells.

An important feature of collenchyma is that it is extremely plastic—the cells can extend and thus adjust to increased growth of the organ. The tissue is found chiefly in the cortex of stems and in leaves and is the primary supporting tissue for many herbaceous plants. In plants with secondary growth, the collenchyma tissue is only temporarily functional and becomes crushed as woody tissue develops. It often constitutes the ridges and angles of stems and commonly borders the veins in eudicot leaves. The “strings” in stalks of celery are a notable example of collenchyma tissue.

Together with sclerenchyma, collenchyma belongs to supporting ground tissues. It is mostly found in leaves and stems. In leaves, it forms strands usually found above and below the midrib and within the petiole. In stems it forms a closed cylinder right beneath the epidermis or under the outer parenchyma layers. It is observed less
frequently in roots. It is a characteristic supporting tissue of the dicots.

Collenchyma derives from the ground meristem, and differentiates usually from parenchyma cells. These cells are elongated and contain living cytoplasm. The long collenchyma cells are oriented parallel to the longitudinal axis of the organ. Their cell wall is composed of cellulose, hemicellulose and pectin. They typically contain a high amount of pectin, the proportion of which component may reach up to 40%. This tissue type of high tearing resistance provides flexibility.

The cell walls of collenchyma cells is considerably but unevenly thickened. On the basis of the thickening pattern, 4 main types are distinguished, among which the first two ones are the most frequent ones:

a. angular: cell walls are most intensely thickened at the corners
b. lamellar: tangential cell walls are considerably, radial walls only slightly thickened (thus the thickened cell walls are visible as lamellar structures under the microscope)
c. lacunar: cell walls adjacent to intercellular cavities are thickened
d. annular: thickened cell walls are ring-like in cross section

**Sclerenchyma**

Sclerenchyma is another type of mechanical ground tissues. It is present in all parts of the plant. It is a long, elongated cell with admirably and evenly thickened cell wall. Into the walls lignin is deposited, what causes the death of the cells. Due to the composition and structure of the cell walls, sclerenchyma provides an inflexible support. These cells may occur individually, scattered among other tissues, but more typically they form strands. It is usually the derivative of parenchyma. Depending on its position, it may be produced by different meristems. Its two main types are the sclerenchyma fibre and the sclereid.

a. **Sclereids** are non-elongated, rather isodiametric cells. They occur scattered or in clusters, mostly embedded in ground tissues. These cells differentiate from parenchyma and have very thick cell walls. Certain sclereid types are named after their shape, e.g. brachisclereids or stone cells are round cells often present in the flesh of fruits. Asterosclereids are star-shaped cells occurring in leaves.

b. **Sclerenchyma fibers** are long, extended cells often with tapering ends. They possess rather small cell lumen and thick wall. Based on their position xilary fibers (within the xylem) and extraxylary fibers (outside the xylem) are distinguished. Xylary fibers develop among the xylem elements and derive from either the procambium or the cambium. Fibers located in any other position are called extraxylary fibers, e.g. the phloem fibers, that are also the products of the procambium or the cambium, but the hypodermal sclerenchyma layers, the sclerenchymatic vascular bundles and the sclerenchyma cap over the phloem are all consist of extraxylary fibers. Sclerenchyma fibers outside the vascular tissues originate from ground meristems. **Sclerenchyma** cells have thick
lignified secondary walls and often die when mature. Sclerenchyma provides the main structural support to a plant.

**COMPLEX TISSUE**

Primary growth produces growth in length and development of lateral appendages. Secondary growth is the formation of secondary tissues from lateral meristems. It increases the diameter of the stem. In woody plants, secondary tissues constitute the bulk of the plant. They take part in providing protection, support and conduction of water and nutrients.

**Xylem**

In most plants, the xylem constitutes the longest part of the pathway of water transport. In a plant 1 m tall, more than 99.5% of the water transport pathway through the plant is within the xylem, and in tall trees the xylem represents an even greater fraction of the pathway. Compared with the complex pathway across the root tissue, the xylem is a simple pathway of low resistance. In the following sections we will examine how water movement through the xylem is optimally suited to carry water from the roots to the leaves, and how negative hydrostatic pressure generated by leaf transpiration pulls water through the xylem.

The Xylem Consists of Two Types of **Tracheary Elements**