Course : BB 404 Development Biology of Plants

Unit : Morphogenesis and Organogenesis in plants

MERISTEMATIC TISSUES

Meristems are populations of small, isodiametric cells with embryonic characteristics. Vegetative meristems are self-perpetuating. Not only do they produce the tissues that will form the body of the root or stem, but they also continuously regenerate themselves. A meristem can retain its embryonic character indefinitely, possibly even for thousands of years in the case of trees. The reason for this ability is that some meristematic cells do not become committed to a differentiation pathway, and they retain the capacity for cell division, as long as the meristem remains vegetative. Undifferentiated cells that retain the capacity for cell division indefinitely are said to be **stem cells**. Although historically called *initial cells* in plants, in function they are very similar, if not identical, to animal stem cells. When stem cells divide, on average one of the daughter cells retains the identity of the stem cell, while the other is committed to a particular developmental pathway.

Stem cells usually divide slowly. Their committed daughters, however, may enter a period of rapid cell division before they stop dividing and can be recognized as specific cell types. Stem cells represent the ultimate source of all the cells in the meristem and the entire rest of the plant— both roots, leaves, and other organs, as well as stems.

The Shoot Apical Meristem

Dynamic Structure

The vegetative shoot apical meristem generates the stem, as well as the lateral organs attached to the stem (leaves and lateral buds). The shoot apical meristem typically contains a few hundred to a thousand cells, although the *Arabidopsis* shoot apical meristem has only about 60 cells. The shoot apical meristem is located at the extreme tip of the shoot, but it is surrounded and covered by immature leaves. These are the youngest leaves produced by the activity of the meristem. It is useful to distinguish the shoot apex from the meristem proper.

The **shoot apex** of the apical meristem plus the most recently formed leaf primordia. The **shoot apical meristem** is the undifferentiated cell population only and does not include any of the derivative organs. The shoot apical meristem is a flat or slightly mounded region, 100 to 300 µm in diameter, composed mostly of small, thin-walled cells, with a dense cytoplasm, and lacking large central vacuoles. The shoot apical meristem is a dynamic structure that changes during its cycle of leaf and stem formation. In addition, in many plants it exhibits seasonal activity, as does the entire shoot. Shoot apical meristems may grow rapidly in the spring, enter a period of slower growth during the summer, and become dormant in the fall, with dormancy lasting through the winter. The size and structure of the shoot apical meristem also change with seasonal activity.

Shoots develop and grow at their tips, as is the case with roots, but the developing regions are not as stratified and precisely ordered as they are in the root. Moreover, growth occurs over a much broader region of the shoot than is the case for roots. At any given time, a region containing several internodes, typically 10 to 15 cm long, may be undergoing primary growth.

Different Functional Zones and Layers

The shoot apical meristem consists of different functional regions that can be distinguished by the orientation of the cell division planes and by cell size and activity. The angiosperm vegetative shoot apical meristem usually has a highly stratified appearance, typically with *three distinct layers of cells*. These layers are designated **L1**, **L2**, and **L3**, where L1 is the outermost layer. Cell divisions are anticlinal in the L1 and L2 layers; that is, the new cell wall separating the daughter cells is oriented at right angles to the meristem surface. Cell divisions tend to be less regularly oriented in the L3 layer. Each layer has its own stem cells, and all three layers contribute to the formation of the stem and lateral organs. Active apical meristems also have an organizational pattern called **cytohistological zonation**. Each zone is composed of cells that may be distinguished not only on the basis of their division planes, but also by differences in size and by degrees of vacuolation. These zones exhibit different patterns of gene expression, reflecting the different functions of each zone. The center of an active meristem contains a cluster of relatively large, highly vacuolate cells called the **central zone**. The central zone is somewhat comparable to the quiescent center of root meristems. A doughnut-shaped region of smaller cells, called the **peripheral zone**, flanks the central zone.

A **rib zone** lies underneath the central cell zone and gives rise to the internal tissues of the stem. These different zones most likely represent different developmental domains. The peripheral zone is the region in which the first cell divisions leading to the formation of leaf primordia will occur. The rib zone contributes cells that become the stem. The central zone contains the pool of stem cells, some fraction of which remains uncommitted, while others replenish the rib and peripheral zone populations.

Meristems Arise during Postembryonic Development

The root and shoot apical meristems formed during embryogenesis are called **primary meristems**. After germination, the activity of these primary meristems generates the primary tissues and organs that constitute the primary plant body. Most plants also develop a variety of **secondary meristems** during postembryonic development. Secondary meristems can have a structure similar to that of primary meristems, but some secondary meristems have a quite different structure. These include axillary meristems, inflorescence meristems, floral meristems, intercalary meristems, and lateral meristems (the vascular cambium and cork cambium).

- **Axillary meristems** are formed in the axils of leaves and are derived from the shoot apical meristem. The growth and development of axillary meristems produces branches from the main axis of the plant.
- **Intercalary meristems** are found within organs, often near their bases. The intercalary meristems of grass leaves and stems enables them to continue to grow despite mowing or grazing by cows.
- **Branch root meristems** have the structure of the primary root meristem, but they form from pericycle cells in mature regions of the root. Adventitious roots also can be produced from lateral root meristems that develop on stems, as when stem cuttings are rooted to propagate a plant.
- The **vascular cambium** is a secondary meristem that differentiates along with the primary vascular tissue from the procambium within the vascular cylinder. It does not produce lateral organs, but only the woody tissues of stems and roots. The vascular cambium contains two types of meristematic cells: fusiform stem cells and ray stem cells.

Fusiform stem cells are highly elongated, vacuolate cells that divide longitudinally to regenerate themselves, and whose derivatives differentiate into the conducting cells of the secondary xylem and phloem.

Ray stem cells are small cells whose derivatives include the radially oriented files of parenchyma cells within wood known as rays.

• The **cork cambium** is a meristematic layer that develops within mature cells of the cortex and the secondary phloem. Derivatives of the cork cambium differentiate as cork cells that make up a protective layer called the *periderm*, or *bark*. The periderm forms the protective outer surface of the secondary plant body, replacing the epidermis in woody stems and roots.

Axillary, Floral and Inflorescence Shoot Meristems : Variants of the Vegetative Meristem

Several different types of shoot meristems can be distinguished on the basis of their developmental origin, the types of lateral organs they generate, and whether they are **determinate** (having a genetically programmed limit to their growth) or **indeterminate** (showing no predetermined limit to growth; growth continues so long as resources permit).

The vegetative shoot apical meristem usually is indeterminate in its development. It repetitively forms phytomeres as long as environmental conditions favour growth but do not generate a flowering stimulus. A **phytomere** is a developmental unit consisting of one or more leaves, the node to which the leaves are attached, the internode below the node, and one or more axillary buds.

Axillary buds are secondary meristems; if they are also vegetative meristems, they will have a structure and developmental potential similar to that of the apical meristem. Vegetative meristems may be converted directly into floral meristems when the plant is induced to flower.

Floral meristems differ from vegetative meristems in that instead of leaves they produce floral organs: sepals, petals, stamens, and carpels. In addition, floral meristems are determinate: All meristematic activity stops after the last floral organs are produced.

In many cases, vegetative meristems are not directly converted to floral meristems. Instead, the vegetative meristem is first transformed into an **inflorescence meristem**. The types of lateral organs produced by an inflorescence meristem are different from the types produced by a floral meristem. The inflorescence meristem produces bracts and floral meristems in the axils of the bracts, instead of the sepals, petals, stamens, and ovules produced by floral meristems. Inflorescence meristems may be determinate or indeterminate, depending on the species.

LEAF DEVELOPMENT

The leaves of most plants are the organs of photosynthesis. This is where light energy is captured and used to drive the chemical reactions that are vital to the life of the plant. Although highly variable in size and shape from species to species, in general leaves are thin, flat structures with dorsiventral polarity. This pattern contrasts with that of the shoot apical meristem and stem, both of which have radial symmetry. Another important difference is that leaf primordia exhibit determinate growth, while the vegetative shoot apical meristem is indeterminate.

Following distinct stages can be recognized in leaf development:

Stage 1: Organogenesis

A small number of cells in the L1 and L2 layers in the flanks of the apical dome of the shoot apical meristem acquire the **leaf founder cell** identity. These cells divide more rapidly than surrounding cells and produce the outgrowth that represents the **leaf primordium.** These primordia
subsequently grow and develop into leaves.

Stage 2: Development of suborgan domains

Different regions of the primordium acquire identity as specific parts of the leaf. This differentiation occurs along three axes: **dorsiventral** (abaxial–adaxial), **proximodistal** (apical–basal), and **lateral** (margin–blade–midrib).The upper (adaxial) side of the leaf is specialized for light absorption; the lower (abaxial) surface is specialized for gas exchange. Leaf structure and maturation rates also vary along the proximodistal and lateral axes.

Stage 3: Cell and tissue differentiation

As the developing leaf grows, tissues and cells differentiate. Cells derived from the L1 layer differentiate as epidermis (epidermal cells, trichomes, and guard cells), derivatives of the L2 layer differentiate as the photosynthetic mesophyll cells, whereas, vascular elements and bundle sheath cells are derived from the L3 layer. These cells differentiate in a genetically determined pattern that is characteristic of the species but to some degree modified in response to the environment

Arrangement of Leaf Primordia

The timing and pattern with which the primordia form is genetically determined and usually is a characteristic of the species. The number and order in which leaf primordia form is reflected in the subsequent arrangement of leaves around the stem, known as **phyllotaxy**.

There are five main types of phyllotaxy:

1. ***Alternate phyllotaxy***. A single leaf is initiated at each Node.

2. ***Opposite phyllotaxy***. Leaves are formed in pairs on opposite side of the stem.

3. ***Decussate phyllotaxy***. Leaves are initiated in a pattern with two opposite leaves per node and with successive leaf pairs oriented at right angles to each other during vegetative development

4. ***Whorled phyllotaxy***. More than two leaves arise at each node.

5. ***Spiral phyllotaxy***. A type of alternate phyllotaxy in which each leaf is initiated at a defined angle to the previous leaf, resulting in a spiral arrangement of leaves around the stem.The positioning of leaf primordia must result from the precise spatial regulation of growth within the apex.