Embryogenesis, Vegetative Growth, and Organogenesis

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The life cycle of all seed plants can be divided into three main stages: embryogenesis, vegetative growth, and reproductive development. During embryogenesis, the single-celled zygote follows a defined pattern of cell divisions and differentiation to form the mature embryo and eventually the seedling, which contains all tissues and organs that develop into the mature plant body. In angiosperms, early phase of the embryogenesis is marked by laying down of the basic body plan of embryo, including establishment of apical—basal polarity and formation of embryonic organs (root and shoot primordial, cotyledons, etc.) and embryonic tissue layers. The embryonic layers – **protoderm**, **ground meristem**, and **procambium**, are the progenitors of the future epidermal, cortical, and vascular tissues, respectively. At the end of embryogenesis phase, several physiological changes occur within the embryos enabling them to sustain the period of dormancy and adverse environmental conditions. Upon the availability of factors like ambient moisture, light, temperature, etc., the seeds germinate, and with accompanying mobilization of stored reserves, the vegetative development commences, wherein tissue primordia in the seedlings grow and cells differentiate. During this period, the meristematic zones corresponding to shoot and root become active. Seedlings display a simple body plan which consists of shoot meristem, cotyledons, hypocotyl, root, and root meristem along the apical-basal axis and a concentric arrangement of tissues along the radial axis: epidermis at the periphery and subepidermal ground tissue and conductive tissue in the center. Vegetative growth is typically **indeterminate**, i.e., with no definite end and characterized by development of lateral organs—the leaves. As the plant undergoes the transition to reproductive development, the shoot apical meristem (SAM) changes shape, becoming an inflorescence meristem, and gives rise to flowers or flowering shoots, thus acquiring a **determinate** growth pattern. Plants exhibit variations in size ranging from a few mm to several hundred meters acquiring the architecture that is suited to the local environment. They grow in size throughout their lives and produce new organs like leaves, flowers, fruits, etc. The growth of plants is defined in terms of increase in number of cells as well as an increase in size

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of cells. It is important to note that this growth is not in terms of increase in dry mass as up to 95% of plant cells is made up of water. Plant growth is accompanied with differentiation of cells, tissues (**histogenesis**), and organs (**organogenesis**) that are specialized structures with distinct functions. Thus, growth and differentiation result in morphogenesis with the plant acquiring an overall form.

24.1 Embryogenesis

Details of embryo development have been studied in several plants using molecular techniques, including the use of mutants, cell-specific markers, etc. Embryogenesis begins with double fertilization in which one sperm cell fuses with the egg cell and another fuses with the central cell to form the zygote and endosperm mother cell, respectively. Embryo development occurs within the highly polarized environment of the ovule. Both, the ovule and the embryo sac, have a distinct polarized axis, and also the egg cell is intrinsically polar as judged from the localization of its organelles on the basal (e.g., vacuole) or apical end (e.g., nucleus).

24.1.1 Acquisition of Polarity

As mentioned earlier, basic features of the body plan, which includes the development of polarity of the embryo and the establishment of the apical-basal axis, are laid down during the early phase of embryogenesis. **Polarity** is the term used to describe the fact that differences can arise along an axis such that one end of the axis is different from the other. Polarity is evident in the embryo sac, egg cell, zygote, and embryo-suspensor complex**.** The zygote undergoes an asymmetric transverse division to form two daughter cells that are unequal in size and follow distinct developmental pathways. In *Arabidopsis*, the larger basal cell develops from the vacuolar region of the zygote, while the smaller upper cell develops from the cytoplasm-rich region. The upper cell then divides to form the embryo proper, while the basal cell forms a single file of typically six to nine cells, the suspensor. This asymmetric division of the zygote is an important factor in the establishment of polarity in morphogenesis. A number of different mechanisms are known to account for asymmetry in the products of eukaryotic cell division, though the precise factors that are responsible for the asymmetry in plant embryogenesis are yet to be identified (Box 24.1). An important factor in the mechanism of cell divisions, which lead to nonequivalent daughter cells, involves the reorganization of actin and associated motor proteins leading to orientation of mitotic spindle. Yet another hypothesis includes the localization of regulatory factors in a specific region of the cell prior to cell division that results in two daughter cells.

Box 24.1: Polarity Induction in *Fucus* Zygote

There are hardly any cells or multicellular systems that are not polarized. One of the few exceptions is the zygote of the brown alga of the genus *Fucus*. The alga is commonly found growing in the upper intertidal shores of temperate oceans. The large-sized (up to 1 mm) egg cells of *Fucus* are released into the seawater, and fertilization occurs in the seawater independent of the maternal influences. The study of ultrastructural details of the egg and early zygote shows these are symmetrical and apolar. As the zygotes develop, the cellular components redistribute in an asymmetrical manner with the zygote now acquiring a distinct polarity. Experimental data has revealed that several factors can affect polarity. Temperature, light, pH value, different chemical gradients, and neighboring *Fucus* zygotes all play a role. The trigger for polarization of the fucoid zygote includes a range of stimuli, including unidirectional light and fertilization. Associated with axis formation, there is an observed localization or redistribution of plasma membrane components, including ion channels, a redistribution of calcium to the basal shaded end, a localization of F-actin at the rhizodermis, and a polarized secretion of Golgi-derived cell wall components toward the "basal" region from which the rhizoid cell will develop.

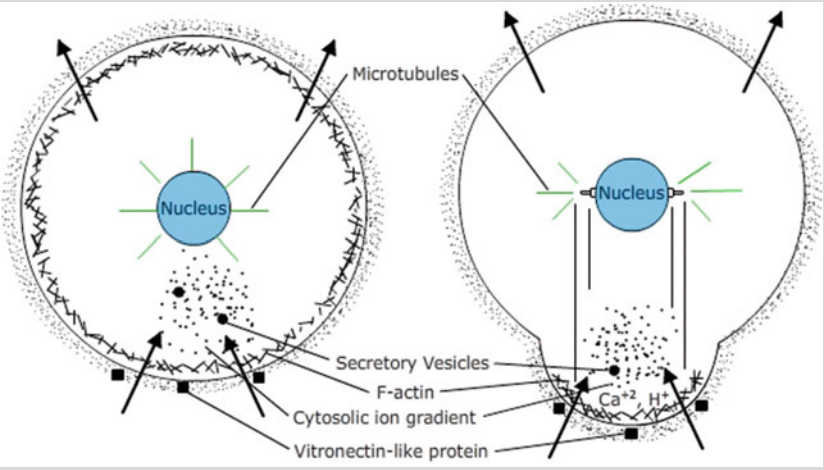


Figure shows axis formation in zygote of *Fucus*. Zygote lacks polarity with more or less uniform distribution of cellular components. As the zygote germinates, these are unevenly distributed along the polar axis. Arrows indicate polar distribution of intracellular constituents.

24.1.2 Stages of Embryo Development

Fertilization induces stretching of the zygote, which is followed by an asymmetric division that gives rise to two daughter cells with different composition, shape, and developmental fate. The apical cell is smaller and densely cytoplasmic, whereas the basal cell is larger and has a big vacuole. The fates of these two cells are dramatically different. Divisions in the apical cell give rise to embryo proper, which goes through several, but continuous, developmental phases in continuity: an eight-celled proembryo is followed by globular, heart-shaped, and torpedo stages. Details of different stages of embryo development have been well described in the model organism *Arabidopsis* (Fig. 24.1):

1. Zygotic stage—haploid egg fuses with sperm to form diploid single-celled zygote.
2. Two-cell stage—asymmetric transverse division of the zygotic cell gives rise to a small apical cell and a larger basal cell.
3. Four-cell stage—apical cell first divides by two longitudinal divisions at right angles to each other.
4. Eight-cell stage—apical cell is further subdivided to form an upper tier and a lower tier of four cells each. The basal cell forms the hypophysis cell and the suspensor.
5. Sixteen-cell (also called dermatogen) stage—tangential cell divisions separate the protoderm that later matures into the epidermal layer from the inner cells.
6. Globular stage—apical cell undergoes a series of cell divisions to generate a globular embryo.
7. Heart stage—divisions on either side of the shoot apical meristem give rise to the two cotyledons, and the embryo now acquires a bilateral symmetry.
8. Torpedo stage—elongation and differentiation of cells along the embryonic axis mark this stage.
9. Mature embryo stage—the embryo enters the dormancy stage, whereby it becomes metabolically inactive and accumulates several storage compounds.

As mentioned earlier the apical cell generates a spherical proembryo, while the basal cell only divides transversally and gives rise to a transient filamentous structure called the suspensor. This extra-embryonic suspensor connects the proembryo to the maternal tissue and pushes it into the lumen of the ovule. Later during embryogenesis, only the uppermost suspensor cell, the hypophysis, becomes incorporated in the embryonic root meristem, as the precursor of the quiescent center (QC) and central root cap cells. The development of embryo in dicots and monocots is identical up to the globular stage. However, later in dicots while the development of the shoot apex continues along the axial axis and the cotyledons develop laterally, in monocots the shoot apex acquires a lateral position, and the single cotyledon is terminal (Table 24.1).

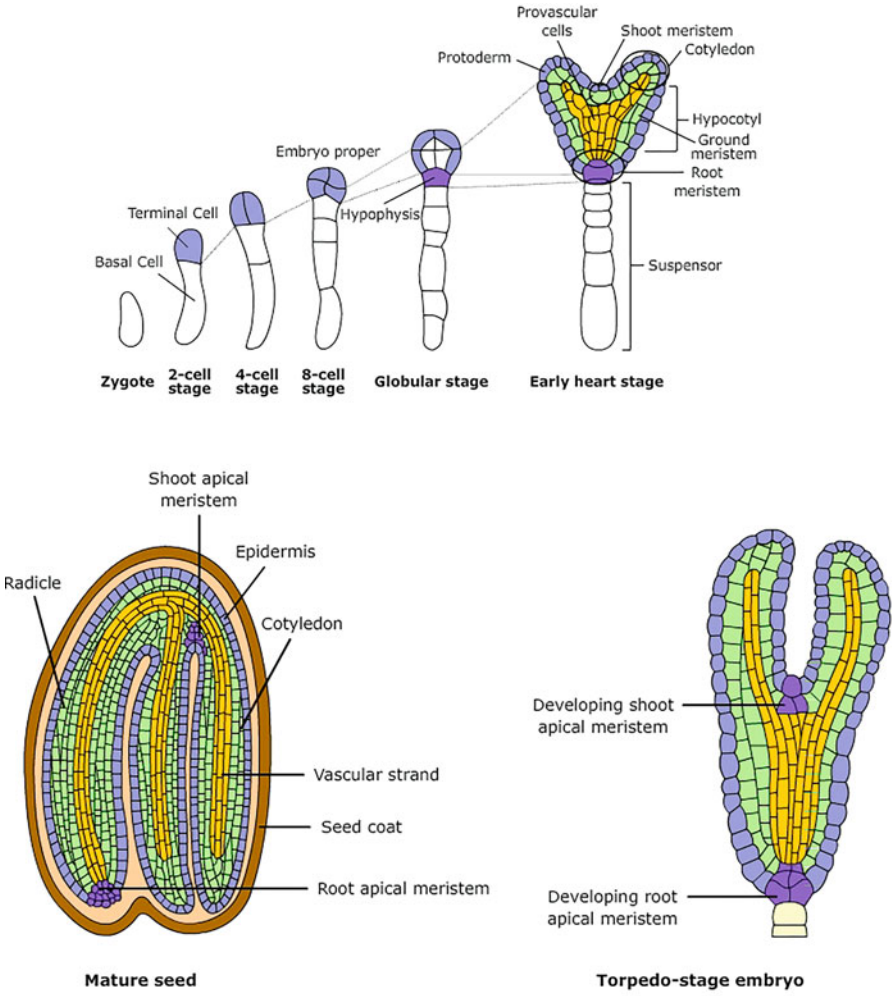


Fig. 24.1 An orderly sequence of events establishes the body plan in *Arabidopsis*

24.1.3 Developmental Patterns

Fate of individual cells within the embryos in animals becomes fixed to produce a defined form. This is defined as lineage-dependent mechanism of embryo development. However, in plants position-dependent signaling mechanisms operate, and the behavior of cells depends on the position of these cells within the developing embryos. Such mechanisms ensure the formation of equivalent forms in spite of having different patterns of cell division.

Table 24.1 A comparison of stages of embryogenesis as observed in *Arabidopsis* (dicot) and rice (monocot)

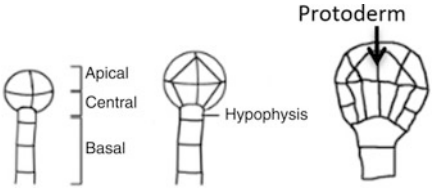
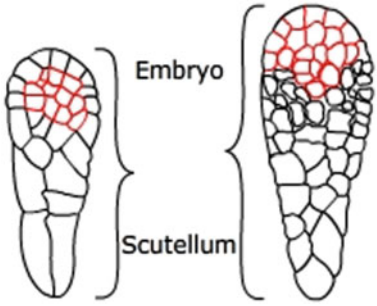
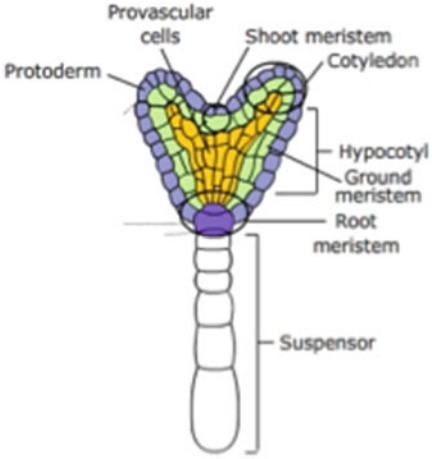
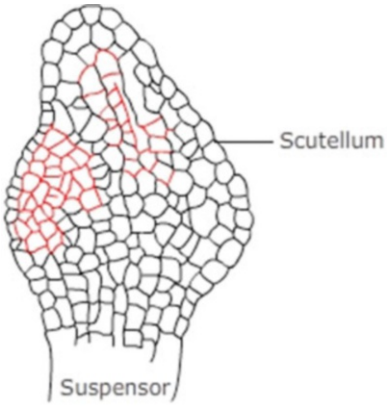
Arabidopsis	Rice
Zygote stage: Single cell stage following fusion of egg and sperm; concludes with asymmetric division (transverse).	Similar
Globular stage: Octant stage followed by formation of spherical protoderm. 	Similar 
Heart stage: Rapid divisions on either side of the future shoot apex producing two outgrowths that later becomes cotyledons. Thus a bilateral symmetry arises. 	**Coleoptile stage**: Formation of (i) coleoptile (ii) SAM (iii) RAM (iv) embryonic root 

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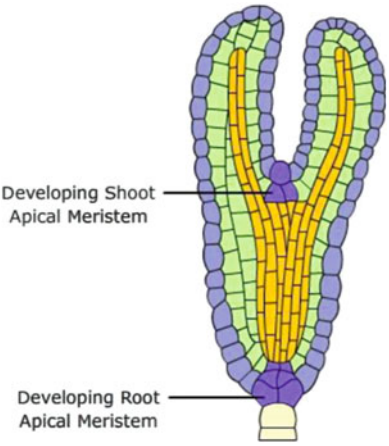
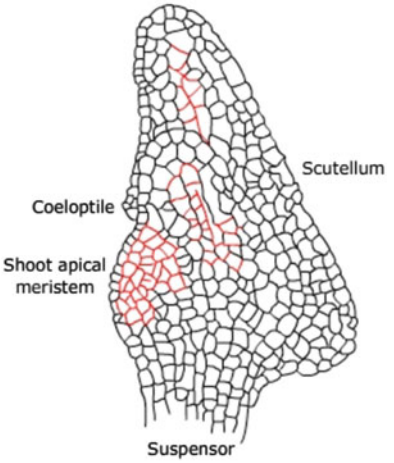
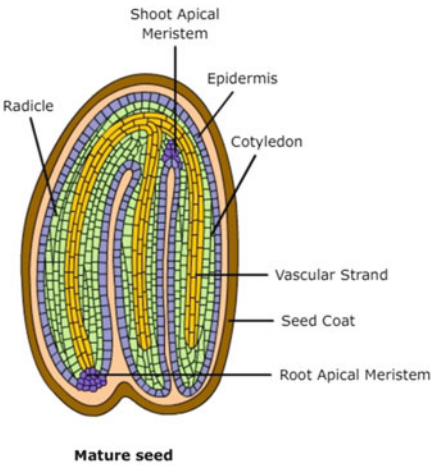
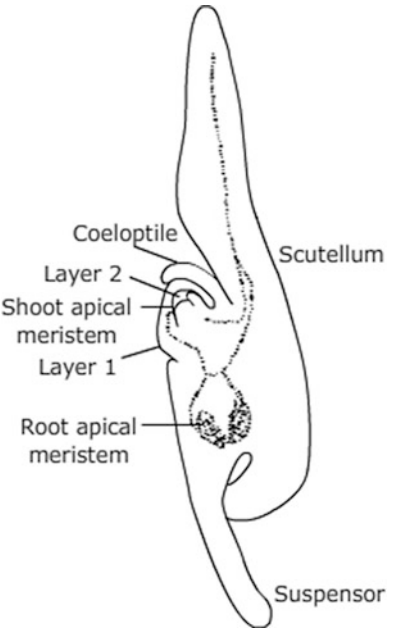
Table 24.1 (continued)

Arabidopsis	Rice
Torpedo stage: Results from cell elongation throughout the embryo axis and further development of cotyledons.  	**Juvenile vegetative stage**: SAM initiates several vegetative leaves. Development of scutellum. Scutellum represents the modified cotyledon specialized to absorb sugars from endosperm during germination. 
Mature stage: The dicotyledonous embryo is oriented along an apical–basal axis and consists of the shoot apical meristem (SAM) located between two cotyledons, a hypocotyl, the primary root and the root meristem.  **Mature seed**	**Mature stage:** The embryonic axis is displaced laterally relative to the scutellum. The SAM is established at a lateral position at the adaxial side of the transition stage embryo opposite to the scutellum. The shoot and root apical meristems at distal ends of the embryonic axis are protected by the coleoptile and coleorhiza, two organs exclusively found in monocots. 

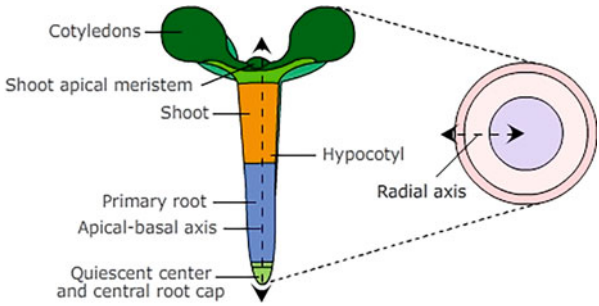


Fig. 24.2 Apical-basal and radial axis of *Arabidopsis* seedling depicted in longitudinal and cross section

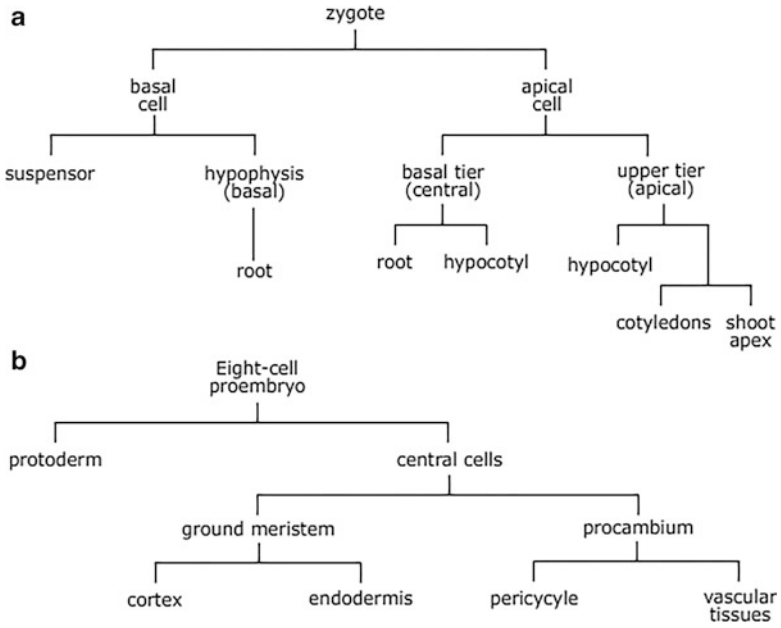


Fig. 24.3 Outline of the two different patterns of development. (**a**) Apical-basal pattern establishes the embryonic organs. (**b**) Radial patterning establishes the primary tissue layers

Two basic developmental patterns are established during embryogenesis (Fig. 24.2):

1. The apical-basal
2. The radial pattern

The polarity of the egg cell precedes the development of the apical-basal axis of the embryo, while the radial axis is established after several cycles of cell division. The apical-basal patterning establishes the main embryonic organs, and the radial patterning establishes the primary tissues (Fig. 24.3).

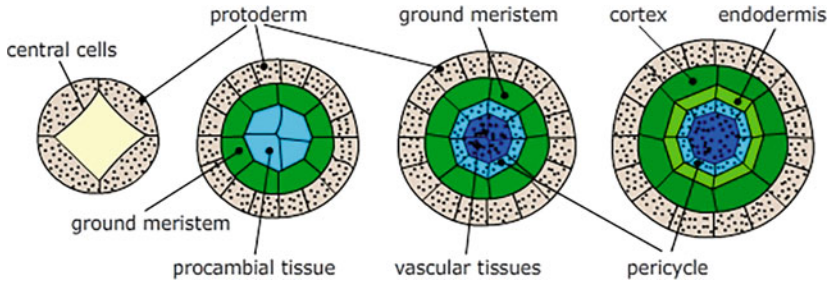


Fig. 24.4 Demarcation of radial pattern in *Arabidopsis*. Periclinal divisions in the octant stage of the embryo separate the central cells from the outer protoderm. Central cells divide to form the ground meristem and the procambial tissues. The ground meristem further gives rise to cortex and endodermis, and the procambial tissues give rise to vascular tissues and pericycle

24.1.3.1 Development of the Axial Axis

The tissues and organs in a typical plant body are arranged along a linear polarized axis with the shoot apical meristem at one end of the axis and the root apical meristem at the other. In the seedlings, this linear array of shoot apical meristem is followed by cotyledons and hypocotyl, and the root with the root apical meristem and the root cap are established during embryogenesis. Different segments of the root possess distinct structural and physiological features. For example, the adventitious roots develop from the lower end of the stem, while shoot buds develop from the apical end even when inverted.

24.1.3.2 Development of the Radial Axis

Radial patterning of the tissues and organs of the plant body is also established during embryogenesis. All cells in the octant stage of the proembryo divide along a tangential plane, aligned along the apical-basal axis. This divides the proembryo in two different regions with different identities: an outer layer of eight cells, the protoderm, which is the precursor of the epidermis, and eight cells in the center of the proembryo, the inner cells, which are the precursors of ground and vascular tissues. A cross section of a root or a stem reveals the presence of three concentric rings of tissues arranged along the radial axis. These include the outermost epidermal layer of cells constituting the epidermis followed by the inner cortical layer (cortex) which encircles the vascular tissues comprising of the endodermis, pericycle, phloem, and xylem (Fig. 24.4).

24.2 Genetic Control of Patterning During Embryogenesis

Genetic and molecular studies using the plant model *Arabidopsis* have opened new arenas of embryo research. The major advances have been based on the analysis of specific mutant phenotypes. These have helped gain an insight into the processes involved in establishing the basic polarity of the embryo. Seedling defective mutants

Table 24.2 Some of the known *Arabidopsis* mutants with aberrant embryogenesis and their functions

Mutant/gene	Functions
GNOM	Apical-basal polarity, vesicular traffic
MONOPTEROS	Encodes auxin-response factor (ARF), controls development of axial axis and vascular tissues
FACKEL	Cell division and growth
ATM 1, *PDF* 2	Protoderm formation
KNOTTED 1	Specification of shoot meristem
SHOOT MERISTEMLESS	Shoot meristem development
WUCHSEL	Maintenance of shoot meristem
CLAVATA 1	Regulation of size of shoot meristem
AINTEGUMANTA	Regulation of size of lateral organs
L1	Specification of L1 layer of tunica
WOL	Vascular tissue specification

are screened to isolate mutations that affect the processes of embryonic patterning. The mutants that affect the essential metabolic activity are avoided. The mutants generated are capable of developing into mature seeds that germinate but display abnormal organization, for example, those with defective apical-basal morphologies. These loss-of-function mutants are indicative of the corresponding genes that are required for normal apical-basal pattern. More than 80 genes with functions in embryogenesis have been examined for tissue expression patterns and interactions. Many genes with functions in pattern formation have been identified by studies of embryogenesis mutants. The genetic analysis of these mutants has allowed development to be modeled as a regulatory network of interaction among various transcription factors. A large number of mutants exhibiting aberrations in embryogenesis are known in *Arabidopsis* (Table 24.2) and a few in some other species such as maize and rice.

24.2.1 Mutants Defining Genes Involved in Axial Patterning

Among the different classes of mutations are the ones with defects in the apical-basal organization of the seedling (Fig. 24.5). These have been given names that indicate the observed mutant phenotypes. *MONOPTEROS* (*MP*) mutant lacks both the central and the basal regions of the seedling, consisting of most of the root and root apex, and so consists essentially of an apical piece of axis to subtend the cotyledons and shoot meristem. The apical structures are not structurally normal and the cotyledons are disorganized. The lower part of the globular embryo that gives rise to hypocotyl and root fails to develop the procambial tissue. Later during development some vascular tissue does develop in the cotyledons, but the vascular strands are not properly connected. The *mp* mutants lack the primary root, but later when they germinate to form seedlings, adventitious roots develop which, however,

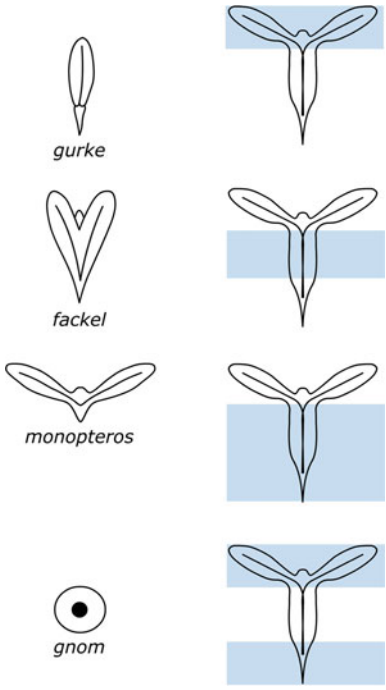


Fig. 24.5 Mutants from *Arabidopsis* with defects in apical-basal organization of the seedling. The shaded area refers to the deleted region

lack well-developed vascular tissues. The *MP* gene is thus essential for the formation of vascular tissue during the postembryonic development. It encodes an auxin response transcription factor (ARF) suggesting an important role in auxin-dependent mechanisms. The activity of ARF is negatively regulated due to their association with repressors like IAA/AUX proteins. Auxin stimulates the activity of their target genes by targeted degradation of the ARF-associated repressors. MP-regulated vascular tissue development therefore results from the auxin-dependent regulation of ARF activities. Additional evidence for such an effect is provided by studies on *BDL* (*Bodenlos*) mutants that exhibit a similar phenotype as *MP* mutants. *BDL* encodes an IAA/AUX repressor that associates with MP to repress its activity, and this effect can be overcome by auxin-induced degradation of BDL. *GNOM* (*GN*) mutants lack both the apical and basal regions including the cotyledons and the root and so consist of a cellular mass with no obvious signs of apical-basal polarity. *GNOM* gene expression is required for the establishment of axial patterning. The gene encodes a guanine nucleotide exchange factor (GEF) that establishes a polar distribution of an auxin efflux carriers (PIN) that are involved in directional transport of auxin. Disruption of GEF activity in *GNOM* mutants disrupts the polar distribution of PIN proteins. The resulting change in the auxin distribution results in developmental defects resulting from the disruption of PIN protein-encoding

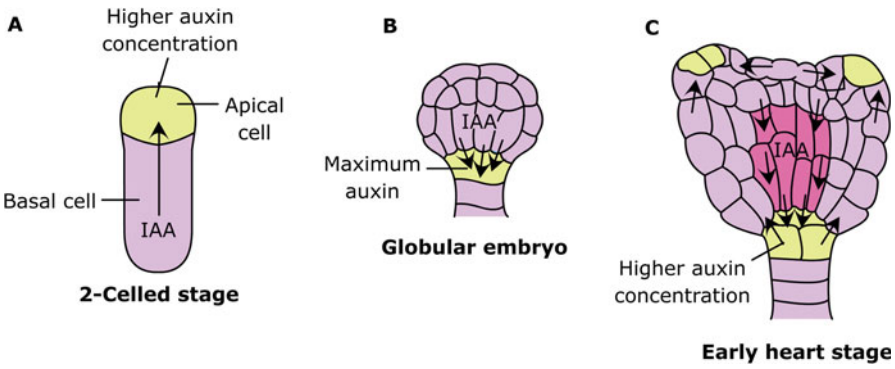
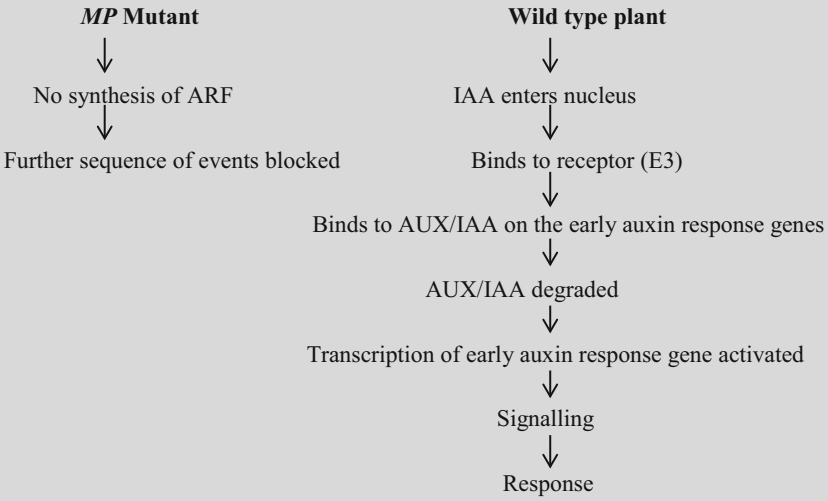


Fig. 24.6 (**a**–**c**) Early stages of embryogenesis are marked by the PIN1-dependent movement of auxin

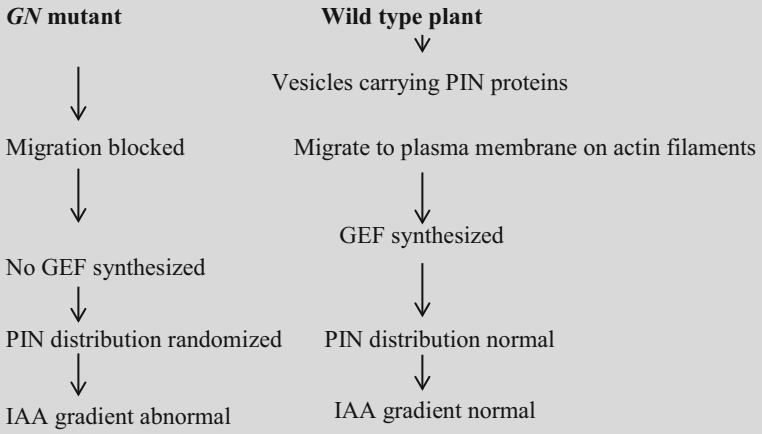
genes. These defects include the apical-basal patterning of the embryo that relies on the polar distribution of auxin in addition to other factors. Preferential accumulation of PIN proteins occurs in the apical cell in the two-celled stage. However, in the later stages of development, the distribution of PIN proteins is reversed, and the PIN proteins accumulate in the basal part of the embryo (Fig. 24.6a, b). As the embryo develops further to the heart stage, the distribution of these proteins becomes complex, and the upward flow of auxin through the superficial layer of cells is balanced by the downward flow in the internal layers (Fig. 24.6c). Both MP and GNOM therefore form a part of the mechanism that guides the auxin-dependent axial patterning of the embryonal axis (Box 24.2). *GURKE* (*GK*) mutants lack the apical region consisting of the shoot apex, the cotyledons, and the upper hypocotyl. The *GK* gene encodes an enzyme—acetyl-CoA carboxylase—that is required for the synthesis of long chain fatty acids and for the formation of pattern in the apical portion of the embryo. *FACKEL (FK)* mutants lack the hypocotyl and so have the cotyledons attached directly to the root. The gene is therefore interpreted to be required for hypocotyl formation and encodes a sterol C-14 reductase. Other genes implicated in embryo development include the *SHOOT MERISTEMLESS (STM)* and *WUSCHEL (WUS)*, which are critical for the initiation of the shoot apical meristem, and *ROOTLESS (RTL)*, which is critical for the initiation of the root apical meristem in the embryo. The expression of *HOBBIT (HBT)* gene is essential for the development of root apical meristem.

Box 24.2: Signaling Events Associated with MP and GN Gene's Action During Embryogenesis

MP encodes Auxin Responsive Factors (ARFs)



GN encodes guanine nucleotide exchange factor (GEF)



24.2.2 Genetic Control of Radial Patterning

Genetic studies have pointed toward several genes involved in radial tissue patterning. Genes like *ATML1* (*ARABIDOPSIS THALIANA MERISTEM LAYER 1*) and *PDF2* (*PROTODERMAL FACTOR 2*) are involved in shoot epidermal cell differentiation and are expressed from early stages of embryogenesis in the protodermal

layers in developing embryos. The mutants for these genes have an abnormal epidermis in which cells display characteristics normally associated with mesophyll cells. Protein products of both the genes appear to be linked to their recognition of a specific eight-base pair recognition sequences shared by the promoters of epidermis-specific genes. These genes encode homeodomain transcription factors and are essential for establishment of normal epidermal identity. Together these genes act to control the activity of downstream genes that mediate the identity of epidermal characters. The binding of ATM1 and PDF2 proteins to the promoters of these genes promotes the transcription of these genes whose active products lead to the differentiation of the epidermis. ATM1 and PDF2 genes contain the same recognition sequence suggesting that their expression is maintained by a positive auto-feedback loop. In roots, genes like *SHR* (short root) and *SCR* (scarecrow) are involved in ground tissue development. *SHR* and *SCR* mutants have defect in the radial tissue pattern. Both produce roots having a single-celled layer of ground tissue. Cells making up the single-celled layer of ground tissue have a mixed identity. While the cells of *SCR* mutants show characteristics of both endodermal and cortical cells, the cells of *SHR* mutants have characteristics of cortical cells and lack endodermal features. The *SCR* mutants also lack the cell layer called the starch sheath, a structure that is involved in the growth response to gravity. The expression of mRNA for *SHR* gene is confined to the layers of vascular elements, but it is required for the formation of the endodermis. It appears that the translated protein is transported into the adjacent external layer where it somehow induces endodermal traits. As endodermal traits are not produced in the vascular tissue (where *SHR* mRNA is produced), the SHR proteins must interact with additional factors that are present in the layer that will develop as endodermis but which are absent in the internal vascular elements. The movement of SHR proteins is mediated by plasmodesmata leading to its inductive effect including promotion of transcription of *SCR*. In association with *SCR*, the *SHR* forms a heterodimer and functions to enhance the genes involved in differentiation of endodermis. The vascular tissue differentiation in roots is established by asymmetric cell divisions that are controlled by *WOL* (*WOODEN LEG*) gene. *WOL* mutants are defective in morphogenesis of vascular tissue in the root and hypocotyl region. These mutants fail to undergo a critical round of cell division that normally produces precursors for xylem and phloem. This defect leads to the development of a vascular system that contains xylem but not phloem elements. WOL also known as cytokinin receptor 1 is one of the several receptors for cytokinins implicating this hormone in the establishment of radial pattern elements. Maturation of embryo also requires specific gene expression. Accompanying the onset of dormancy is the shutting down of gene transcription and protein synthesis. Additionally, expression of specific genes like *ABI3* (*ABSCISIC ACID INSENSITIVE 3I*) and *FUSCA3* genes are essential for initiation of dormancy. These genes are sensitive to the hormone abscisic acid which is known to be the molecule involved in signaling that initiates dormancy. The *LEC1* (*LEAFY COTYLEDON1*) gene which is active during late embryogenesis is another gene involved in embryo maturation. It acts as a repressor of vegetative development, and its expression is required throughout embryogenesis.

24.3 Role of Auxin in Establishing Polarity During Embryogenesis and Vegetative Development

Auxin plays a critical part in embryogenesis, providing positional information for the coordination of correct cellular patterning from globular stage onward. The term **morphogens** is used for auxins and its synthetic analogs since these can induce the formation of embryos from somatic cells and can induce responses in target tissues in a concentration-dependent manner. The main sites of synthesis of auxin are the shoot meristems and leaf primordia. The polar auxin transport is important for modulation of several key responses. The polar auxin transport is thus created by a combination of localized synthesis and intercellular processes. Auxin controls much of postembryonic development, including plant architecture through the modulation of meristem activity, organogenesis, vascular tissue differentiation, tropic growth, etc., in response to environmental factors. The movement of auxin toward the root apex and the shoot apex is referred to as rootward and shootward transport. This polar transport of auxin occurs in cell-to-cell manner across the cell wall and plasma membrane of adjacent cells, and the overall process requires expenditure of energy. The polar auxin gradients are initially established by auxin synthesized locally, but later these gradients are extended with the directed auxin transport by specific transporter proteins present on the plasma membrane.

The chemiosmotic theory proposes that auxin requires an **influx** and **efflux** carrier proteins in order to move through cells and tissues. In *Arabidopsis* roots the AUX1 proteins have been identified as the influx carrier, while the PIN proteins (named after the pin-shaped inflorescences formed by the *pin1* mutant of *Arabidopsis*) constitute the putative transport protein of the efflux carrier complex. A crucial feature of the polar transport model is that the auxin efflux carriers are localized at the basal ends of the conducting cells. The auxin flow is therefore determined by the differential cellular positioning of the PIN proteins. Several *PIN* genes have been identified, and more than ten different *PIN* homologues have been found in *Arabidopsis*. *PIN* genes have also been identified in maize, rice, and poplar, and the high degree of conservation between the monocot and dicot species indicates that the PIN proteins have a conserved function throughout the plant kingdom. In *Arabidopsis* members of this family of transporters have different expression patterns within time and space and so offer the plant a means by which auxin can be transported precisely (Fig. 24.7). *PIN1* mediates organogenesis and development of vascular tissue and is located at the basal end of cells within the vascular stele. Gravitropic growth of roots is mediated by *PIN2*; differential growth of shoots is controlled by *PIN3*. *PIN4* regulates the activity of the root meristem, and the early embryo development is mediated by *PIN7.* Auxins provide the positional information to a developing and patterning tissue. Studies on the *POLARIS* gene of *Arabidopsis* provide further information on the role of auxin in defining position and cell activities during embryonic and seedling root development. It encodes a very short transcript that appears to regulate root sensitivity to ethylene and to modulate root growth. The *POLARIS* gene promoter is upregulated by auxin very rapidly, within minutes, and its spatial expression pattern represents a useful marker

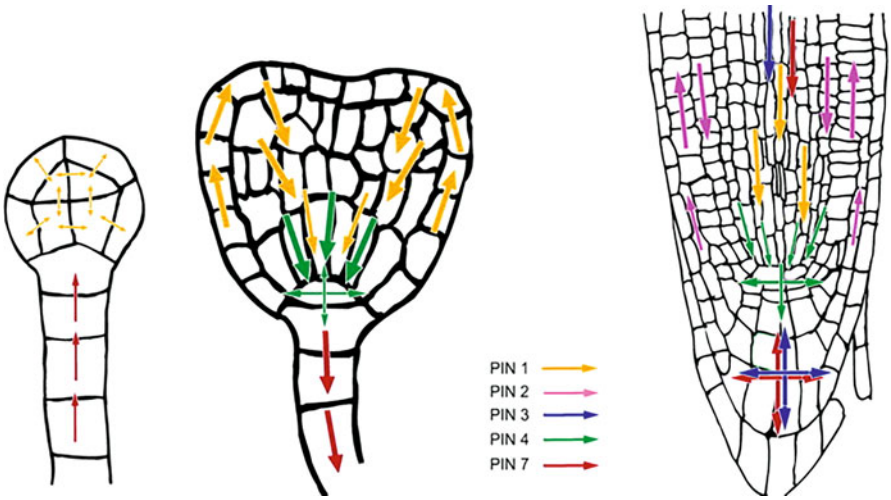


Fig. 24.7 *PIN* gene expression and polar localization in preglobular, early heart embryos and in seedling root. Arrows indicate presumed directions of auxin flow based on subcellular PIN polarity

of auxin localization in the root. Interestingly, correct spatial patterning of *POLARIS* expression is disrupted significantly only in the most severe, ball-shaped *gnom* seedlings, suggesting that these individuals, but not the more conical-shaped *gnom* seedlings, are defective in polar auxin transport. This is consistent with the observed defective PIN1 localization in *gnom* embryos and suggests that auxin provides a chemical framework for the patterning of apical-basal gene expression and cellular activity in both embryo and seedling.

24.4 Plant Development and Meristems

Cell division in plants is localized in meristems that act as source of cells for the formation of new tissues and organs. Meristems can be defined as a group of cells that retain the capacity to proliferate and whose ultimate fate remains undetermined. Based on the position, several types of meristems are distinguished: (1) *shoot apical meristem* (*SAM*) and (2) *root apical meristem* (*RAM*). Shoot and root apical meristems are formed in embryogenesis and are called **primary meristems.** The primary tissues and organs that comprise the primary plant body arise from these primary meristems. Meristems that arise later during the postembryonic phase of development are called as **secondary meristems**. These include the axillary, inflorescence, floral, intercalary, and lateral meristems (vascular cambium and cork cambium). (1) Axillary meristems—these are derived from the shoot apical meristems and are formed in the axil of leaves. (2) Intercalary meristem—it

represents meristematic region within the developing organs, and these enable further localized growth (e.g., at the base of elongating grass leaves). (3) Meristemoids—they arise in differentiated region such as leaves to give rise to specific structures such as stomata. (4) Vascular cambium—these are secondary meristems that develop from procambium within the vascular cylinder. Two types of cells are distinguished in the vascular cambium—the **fusiform** and **ray initials**. While the former gives rise to the conducting cells of secondary xylem and phloem, the latter are divided to form the parenchyma cells arranged in radial files (rays). (5) Cork cambium—these are secondary meristems that develop in the cortex and the secondary phloem and give rise to outer protective periderm or bark of the secondary plant body.

Apical meristems localized in the tips of stems (SAM) and roots (RAM) contribute toward growth of the apical-basal axis of the plant. These meristems contribute toward the formation of primary meristems like the **periderm**, the **procambium**, and the **ground meristem** that are the source of epidermis, vascular tissue, and ground tissues, respectively. The apical meristems are organized into distinct regions. Although the meristems—SAM and RAM—differ in their anatomical characteristics and the organs or cells that are produced, the basic organization is similar. In both, an organizing center (OC in the shoot meristem, QC in the root meristem) is surrounded by stem cells (also called as initial cells in plants) for various tissues. These stem cells remain undifferentiated and retain the capacity for cell divisions indefinitely and are not committed to a differentiation pathway.

24.4.1 Shoot Apical Meristem

The shoot apical meristems (SAM) comprise of the central region (CZ), the peripheral zone (PZ), and the rib zone (RZ). The central zone (CZ) is located at the summit of the SAM and contains the slowly dividing stem cell population. This region does not consist of permanent initial cells but rather acts as a reservoir through which individual stem cells pass. Stem cell division replenishes the CZ and displaces the daughter cells outward into the surrounding PZ, where cells are rapidly dividing and new organs are initiated, as well as downward into the RZ that provides cells for the internal tissues of the stem and lateral organs. At the top of the RZ is positioned a small group of cells called the organizing center (OC), which acts as a niche that sustains the overlying stem cell reservoir. Although clear boundaries between the three domains have not been observed, expression studies reveal that the cells in each zone have different gene expression patterns and thus distinct molecular as well as functional characteristics. Classical studies indicate that the angiosperm SAM is organized into overlapping cell layers and domains (Fig. 24.8). The *Arabidopsis* SAM consists of three cell layers, L1–L3, which remain clonally distinct from one another due to their specific cell division patterns. The single-layered L1 and L2 cells comprise the **tunica** and divide anticlinally, perpendicular to the plane of the meristem. These cell layers generate the epidermis and subepidermis, respectively, of the shoots, leaves, and flowers. The multitiered L3 cells comprise the **corpus** and

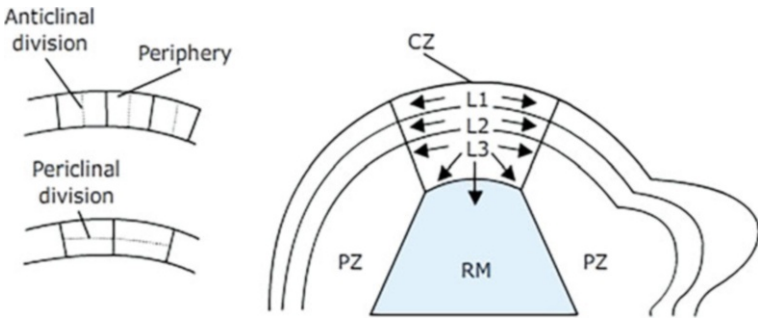


Fig. 24.8 Shoot apical meristem is distinguished into distinct zones. L1, L2, and L3 represent successive layers of the CZ. *CZ* central zone; *PZ* peripheral zone; *RM* rib meristem

divide in all planes, forming the internal tissues such as the stem vasculature and pith. SAM produces leaf **primordia** that develop into new leaves and cells that will produce lateral (axillary) bud primordia, which have the potential to form new branches, in the axils of leaves. The SAM is initiated within the apical half of the proembryo and as such does not involve cell-cell signaling across the apicobasal boundary. Many factors are known to control aspects of shoot meristem function, but the vast majority of these act in the homeostatic control of meristem size rather than the initiation of the meristem. The OC cells and the overlying stem cells mutually control the size of the other population, leading to a stable meristem size. The installation of the OC and stem cell area occurs during the mid-globular stage, and both are maintained throughout plant life. It is important to note that the identities and the characteristic patterns of division of different initial cells are determined by their position rather than their genetic programming.

24.4.2 SAM Development: Role of Auxin and Transcription Factors

SAM develops at a position where auxin is low. Auxin activity in embryo development leads to the formation of terminal domains maintained in pluripotent state, i.e., capable of differentiating into many cell types. It leads to the formation of stem cells, which are cells that are undifferentiated and which can both perpetuate themselves and give rise to daughter cells capable of differentiating into specialized cells. SAM development is related to auxin-related gene activities. PIN-mediated auxin flow directs auxin to regions that flank SAM, while the central zone becomes relatively auxin-deficient. The early embryogenesis is marked with the accumulation of PIN1 protein in the apical regions. This is however reversed to the basal region in the early heart stage. The change in the concentration is mediated by the phosphorylation on PIN proteins by kinases like PINOID and phosphatase PP2. The effect is also affected by the alteration in the transcription of several genes that are involved in the distribution of PIN proteins. Four genes (auxin related) are responsible for SAM development:

1. *MP (MONOPTEROS)*: leads to differences in auxin activity in central and flanking regions. *MP* expression is relatively weak in central region of the apex but stronger in flanking regions, which will later develop into cotyledons.
2. *WUS* (WUSCHEL) genes: these express in the subapical region in the early 16-cell stage of embryo development. These play an important in specifying and maintaining the identities of initials in the SAM.
3. *CUC* (Cup-shaped cotyledon): expressed in central region between the cotyledons, and it helps in the development of cotyledons. *CUC* mutants have no cotyledon development.
4. *STM* (Shoot meristemless) gene: the expression of *STM* gene coincides with *CUC* expression and is confined more around the central region. Both *CUC* and *STM* mutants have similar phenotypes.

Both *CUC* and *STM* help to maintain the initial cells in a proliferative state. The expression of these two genes in the central region of the SAM is related to the low auxin concentration in this region as compared to the flanking regions. This auxin-dependent patterning in the shoot apex is thus related to the low levels of auxin in the SAM and the intercotyledonary regions and the related high expression of CUC in these regions (Fig. 24.9). An opposite pattern is seen in the cotyledon primordia. Mutations in *MP* and *NPH4 (NON PHOTOTROPIC HYPOCOTYL 4)* block the auxin signaling in the cotyledonary region which leads to ectopic expression of CUC genes in this area. This further initiates the localized expression of *STM* gene and later the *CLAVATA3* (*CLV3*). The latter plays an important role in limiting the number of apical initial cells in the SAM. The movement of auxin away from the central region of SAM along with the upward flowing stream of auxin results in auxin accumulation in the tips of the growing cotyledons and it further flows down into the hypocotyl. This directional transport of auxin results in the activation of ARF proteins MP and NPH4, which are involved in the differentiation of vascular tissues.

24.4.3 Root Apical Meristem

The root apical meristem has a simple structure with distinct zones (Fig. 24.10):

1. Root cap (RC): At the distal tip of the root is the root cap, consisting of the central columella (COL) and lateral root cap (LRC).
2. Meristematic zone (MZ): Located just beneath the root cap, it consists of a group of initials that divide and differentiate to form the mature tissues of the root. The MZ can be divided in two zones: the apical MZ, consisting of the most actively dividing cells, and a basal MZ, in which cells become larger, divide less frequently, and begin to acquire distinct fates. The RC can thus be distinguished into RC meristem (RCM) and, the main, proximal meristem (PM).
3. Zone of elongation: As cells exit mitosis, they leave the MZ and undergo a period of elongation, thereby defining the elongation zone (EZ). The rate of cell division progressively decreases as the distance from the apical meristem increases.

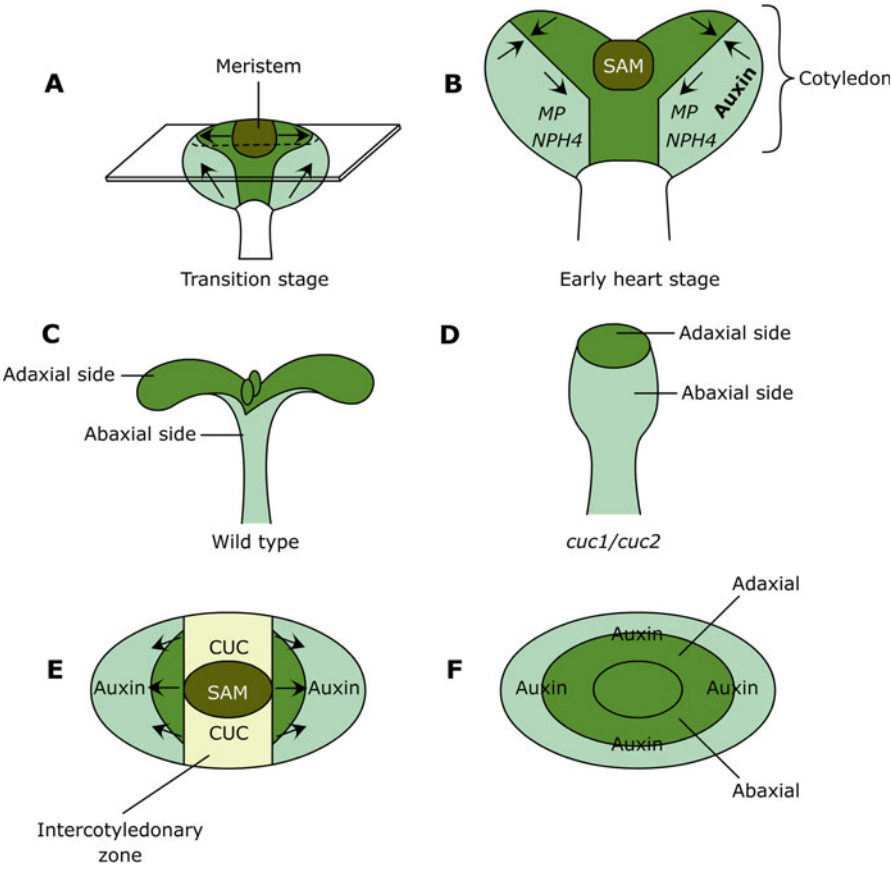


Fig. 24.9 Patterning in the shoot apex is dependent on relative auxin concentrations in the central region versus in the flanking region of the developing shoot apex. (**a**, **b**) Arrows depict the flow of auxin in the transition and the early heart stage. The auxin-dependent genes such as *MP* and *NPH4* are thereby differentially regulated in these regions to promote patterning in these regions. (**c**) and (**d**) represent the morphological features of the wild-type and *cuc* mutants. (**e**) and (**f**) represent a cross-sectional view of the wild-type and *cuc* mutants, respectively

4. Zone of maturation: Finally, cells cease elongation and enter the differentiation zone (DZ), which is typically defined by the appearance of root hairs and vascular cells with visible secondary cell wall formation.

Located just above the RC lies the **quiescent center** which is so named because of the relatively low rates of cell divisions that occur in this region in comparison to surrounding tissues. The close association between the cells of the QC and the initial cells in the MZ suggests a functional interdependence between the two. Experiments involving surgical removal of QC leads to disruption of normal cell division and

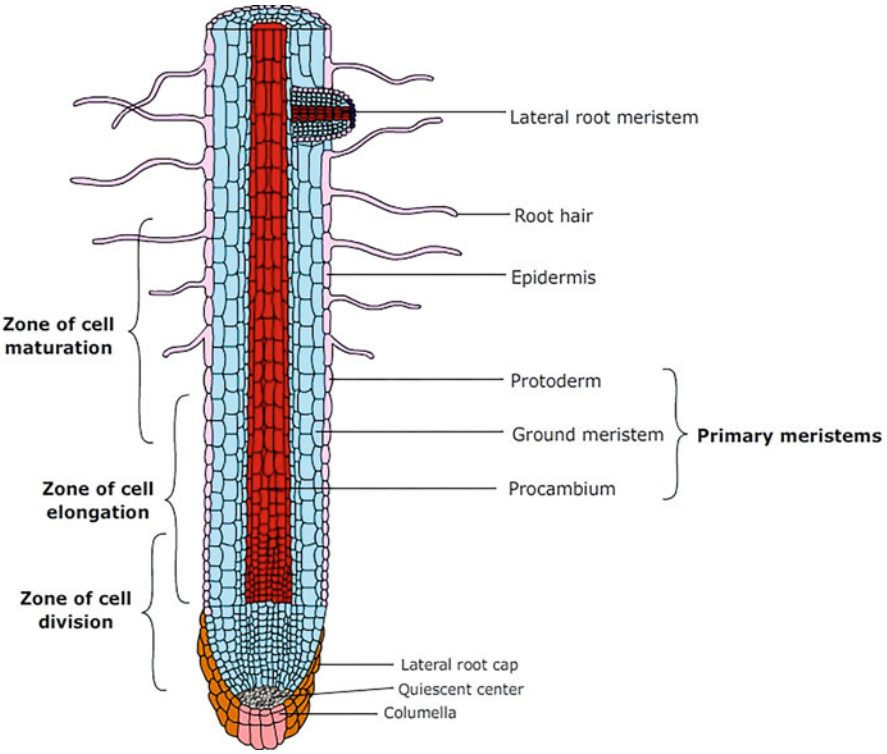


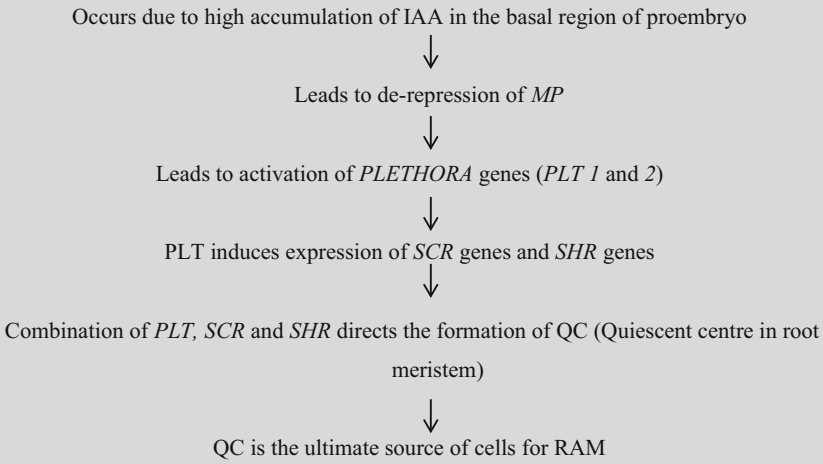
Fig. 24.10 Diagrammatic sketch of longitudinal section of a typical root

precocious differentiation in the adjacent initial cells. This suggests that as proposed for the SAM, position-dependent mechanisms also play an important role in specifying the different cell types in RM.

24.4.4 Role of Auxin and Cytokinin in Establishment of RAM and Root Development

Auxin plays an important role in the determining the complex structure and function of RAM. A higher concentration of auxin is found in the QC. A shift in the position of auxin maxima on using chemical treatments leads to a corresponding change in the position of QC. A gradient of auxin occurs across the root and is responsible for a number of responses including localized areas of cell division and cell differentiation (Box 24.3). Auxin triggers the breakdown of transcription repressor of *MP (MONOPTEROS)* the IAA/AUX. MP encodes ARF that has an auxin-dependent role in maintenance of root structure in vegetative growth. Several transcription factors act downstream to the MP and coordinate the specific growth of roots. These include the PLETHORA 1 (PLT1) and PLETHORA 2 (PLT2) that belong to the AP2/ETHYLENE RESPONSIVE FACTOR class of proteins. The accumulation of

Box 24.3: Genetic Regulation of RAM Development



auxin in the QC activates the expression of *PLT1* and *PLT2* genes. Auxin thus provides the positional signal for specific transcriptional programs to be switched which further determine and contribute toward the establishment and maintenance of RAM. Another class of genes sensitive to auxin flux and which plays an important role in RAM are the *WOX* (*WUSHCHEL*) genes. Similar to the *WUS* genes that operate in the SAM, the *WOX* helps to maintain the population of undifferentiated initials in the QC and prevents their premature differentiation.

Another class of hormone cytokinin is also known to play an important role in normal root development. While auxin is synthesized in the shoot and transported toward the roots, the cytokinins are synthesized in the root and then moves toward the shoot. Cytokinin signaling begins during early phase of root development in the hypophysis of the globular embryo. As the hypophysis divides in two, the basal cell loses the cytokinin expression, while the apical cell retains it and in fact divides to form the QC. Auxin on the other hand has a reverse expression. This supports the premise that the two hormones have an opposing effect in shoot and root development. The loss of cytokinin expression in the basal cell is due to activity of two genes *ARR7* and *ARR15* that have auxin response elements (AuxRE) in their promoters. Antagonistic activity of cytokinin and auxin in the basal cell is essential for normal development of RAM and enables the particular pattern of cell divisions that occur in the QC.

24.5 Growth and Differentiation of Lateral Roots

The architecture of a plant's root system is important for carrying out its functions. The **radicle** of the seedling together with the lateral (branch) roots it produces constitutes the primary root system of the plant. The root systems of most vascular plants are formed by branching of **lateral roots** (LRs) from a **primary root** (PR) that first develops during embryogenesis. Root hairs, each of which is an outgrowth of a single epidermal cell, provide most of the surface through which roots absorb water and dissolved minerals. Stems and leaves may have the ability to produce **adventitious roots**. In this case, adventitious root primordia originate from parenchyma cells that are adjacent to vascular bundles. The roots of monocots and dicots are similar in some features and also differ in certain characteristics. While they have roughly similar features like the embryonically derived primary root, lateral roots, and adventitious root, they differ significantly in the type of root systems they possess. The monocot root system consists of a primary root that develops from the radicle and adventitious or **seminal roots** that branch from the scutellar nodes. Also present are the postembryonically developed crown roots or **prop roots** that develop from the lower most nodes of the stem. These prop roots unlike the primary and seminal roots develop and branch throughout the vegetative growth of the plant and make up the majority of the root system in monocots. In dicots, the root system consists of the main primary or tap root and its branches. Additionally, adventitious roots arise from the subterranean stems or from the hypocotyl. Root hairs perform the important function of water and nutrient uptake in plants. Additionally, they also serve to anchor plants to soil. The initiation and growth of lateral roots has been studied in detail in several flowering plants. Three patterns of root hair differentiation have been seen in plants. Type I pattern is one in which all the cells of the root epidermis have the potential to form root hairs. Majority of the plants exhibit Type I root hair development pattern. The other types include those in which some of the cells have the potential to form root hairs (trichoblasts) and some cells are incapable in forming root hairs (atrichoblasts). These are further divided into Type II, in which the cells of the root meristems divide by an asymmetric division and the trichoblast is formed from the smaller cell. Examples of plants exhibiting Type II pattern of root hair development include the primitive vascular plants *Lycopodium*, *Selaginella*, etc. Type III is exhibited by members of the Brassicaceae family in which trichoblasts and atrichoblasts occur in alternate files. LRs initiate from a specialized cell layer in the pericycle overlying the developing xylem tissue (Fig. 24.11). LR development involves stimulation and dedifferentiation of pericycle founder cells, which increase in size, reenter the cell cycle, and divide asymmetrically to give rise to a lateral root primordium (LRP), which then emerges through the outer layers of the PR. The endodermis, the cell layer immediately overlying the pericycle, has recently been identified as a key regulator of LR developmental progression. Feedback from the endodermis to the pericycle is required for LR initiation. LR development and changes in root architecture are brought about through a combination of hormone signaling, environmental cues, and hormone-independent protein activity. The initiation and growth of lateral roots are controlled by the concentration and transport of

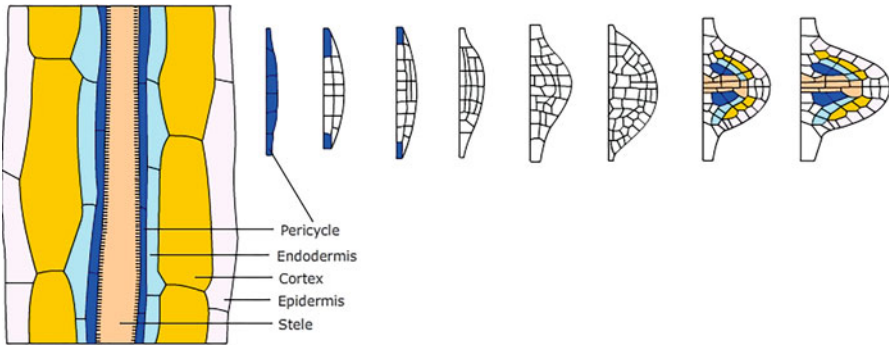


Fig. 24.11 Stages of development of lateral roots which originate from pericycle of the primary root

plant hormones, particularly auxin. Some of the key genes regulating lateral root development are auxin-independent, however. Molecular genetic studies using *Arabidopsis* mutants have revealed that the auxin transport system with a balance of influx and efflux is important for LR initiation and subsequent LR primordium development. In addition, normal auxin signaling is mediated by two families of transcriptional regulators, Aux/IAAs and ARFs, which are necessary for LR formation. Gain-of-function Aux/IAA mutants have altered auxin sensitivity and pleiotropic defects in growth and development that include differences in lateral root formation. Auxin synthesized in the aboveground part of the plant is transported to the roots; more recent work has revealed that some auxin is also synthesized in the roots themselves. Auxin is transported directionally within roots in a process known as polar auxin transport. Auxin moves toward the root tip in cells associated with the vascular cylinder (stele) and moves away from the tip in cells of the epidermis. Localized auxin concentrations are regulated both by diffusion across membranes and by the action of several auxin transport proteins; these include AUX1, which facilitates influx of auxin into cells, and PIN, which controls auxin efflux. Taken together, the actions of these proteins establish local auxin maxima as well as concentration gradients, and it is in the areas of these maxima that lateral roots are initiated. Any mutation that prevents the establishment of normal auxin gradients disrupts the patterning of root development. The promotion of lateral root formation by auxin is inhibited by cytokinins (CKs), which act directly on the lateral root founder cells in the primary root to bring about this inhibition. There is evidence that cytokinin may interfere with PIN gene expression.

The role of auxin in initiating and maintaining the quiescent center of the maize root meristem is hypothesized to be mediated through the variation in the enzyme ascorbic acid oxidase (AAO) which is involved in the breakdown of ascorbic acid. Ascorbic acid is a compound which is necessary for the transition from G_1 to S phase in the cell cycle, and which is broken down by AAO. Formation of AAO is increased in response to auxin in the quiescent center than surrounding cells. Auxin influences

AAO levels within the root meristem and that this ensures the continued stem cell ability of the quiescent center.

Proteins like ALF4, ARABIDILLO-1, and ARABIDILLO-2 are known to promote lateral root initiation in an auxin-independent manner. The aberrant lateral root formation *ALF4* mutation in *Arabidopsis* blocks the initiation of lateral roots, thus greatly altering root system architecture. The *ALF4* mutant completely lacks lateral roots, and it appears that the cell cycle in pericycle cells is blocked in the mutant plants. ALF4 protein functions in maintaining the pericycle in the mitotically competent state needed for lateral root formation.

24.6 Cell Growth and Differentiation

An essential feature of plant development is the ability of plant cells to grow and differentiate. **Growth** of an organism is defined as an irreversible increase in mass. Because mass is related to cell volume and cell number, growth refers to an irreversible increase in cell size (enlargement) or to an increase in cell size as well as cell number (cell division). Cell division, by itself, is not sufficient to result in growth. **Differentiation**, in contrast, refers to the cells acquiring qualitative differences among other cells of common origin, i.e., those derived from a cell or group of cells. It is by differentiation that cells in an organ or tissue become different from each other or specialized for different functions, e.g., the epidermis, or mesophyll, or xylem or phloem cells in a leaf. **Morphogenesis** is the acquisition of form, how a plant or organ acquires its distinctive shape or form. The control of these two processes is central to a study of plant morphogenesis.

The growth and development in higher plants involves cell division, expansion, and differentiation along the apical-basal axis and the radial axis. The radial axis especially in dicotyledonous species grows in size as the concentric rings of new cell layers are added following cell divisions in the vascular cambium of seedling stem, hypocotyl, and roots. On the other hand, development of the apical-basal axis involves meristems like the shoot apical meristem and the root apical meristem and includes patterning of symmetry and formation of functionally distinct structures. This meristematic activity of plant cells is based on the essential property of every plant cell—**totipotency**—i.e., the ability of the plant cells to divide, grow, and differentiate into whole organisms. **Differentiation** refers to differences, other than size, that arise among cells, tissues, and organs. Differentiation occurs when cells assume different anatomical characteristics and functions or form patterns. Differentiation begins in the earliest stages of development, such as when division of the zygote gives rise to cells that are destined to become either root or shoot. Later, unspecialized parenchyma cells may differentiate into more specialized cells such as xylem vessels or phloem sieve tubes, each with a distinct morphology and unique function. The plant cells exhibit extreme plasticity with their ability to differentiate, dedifferentiate, and redifferentiate, i.e., even though some plant cells may appear to be highly differentiated or specialized, they may often be stimulated to revert to a more embryonic form. For example, mature somatic cells isolated from any body

part of the plant, cultured on an artificial medium, may be stimulated to reinitiate cell division, to grow as undifferentiated **callus** tissue, and eventually to give rise to a new plant. It is as though the cells have been genetically reprogrammed, allowing them to reverse the differentiation process and to differentiate along a new and different path. This ability of differentiated cells to revert to the embryonic state and form new patterns without an intervening reproductive stage is called totipotency. Plants can therefore be propagated indefinitely in the vegetative state.

24.6.1 Cell Growth: Role of Wall Extensibility

Growth of cells derived from meristems is accompanied by cell enlargement mediated by water uptake. An essential requirement for such increase in cell volume requires wall extension, which is related to turgor pressure. Wall extension is related to turgor pressure and is a quantitative measure of the capacity of the wall to irreversibly increase its surface area. Turgor pressure develops because the cell wall resists the force of the expanding protoplast pushing against the wall, which thus generates stress within the wall. However, in order to prevent excessive water uptake and to avoid rupturing the plasma membrane due to high turgor pressure, plant cells are surrounded by a very strong and relatively rigid wall. The strength and rigidity of the cell wall impose critical restrictions on the capacity of plant cells to grow. The ability of cell wall to extend is essential for plant cell growth and morphogenesis. Modification of cell wall strength and rigidity is essential in order to change the water potential of the cell, permit water uptake, and, consequently, allow the cell to enlarge. Plant cell wall is a composite polymeric structure comprising of cellulose microfibrils coated with heteroglycans (hemicelluloses such as xyloglucan) and embedded in a dense, hydrated matrix of various neutral and acidic polysaccharides and structural proteins. Plant cell walls have the ability to extend at acidic pH. This pH-dependent extension is known as acid growth. Cell wall proteins such as **expansins** that are activated by acidification at pH between 4.5 and 6 disrupt noncovalent binding between cellulose and hemicelluloses. Other wall proteins such as xyloglucan endotransglycosylase/hydrolases (XTHs) which hydrolyze glycosidic bonds also contribute to wall loosening by modifying wall properties. Acid growth is mediated by an auxin-stimulated proton pump in the plasma membrane, which decreases the pH of the cell wall solution, promoting the activity of wall-loosening proteins (Fig. 24.12). Within minutes of treatment with auxin, there is induction of rapid cell elongation in stem, coleoptile, and hypocotyl segments. This rapid effect is believed to result from the activation of a proton pump ATPase at the plasma membrane, inducing extrusion of H^+, extracellular acidification, activation of expansins, and subsequent wall loosening. Activation of the plasma membrane H^+ ATPase causes hyperpolarization of the membrane potential and activation of voltage-dependent K^+ inward channels. Uptake of K^+ is likely to contribute to the water uptake necessary to sustain expansion. In addition to the stimulation of their activity, auxin also induces expression of both H^+ ATPase and K^+ channels. Two types of modes of cell expansion are there in plants: diffuse and tip growth. The

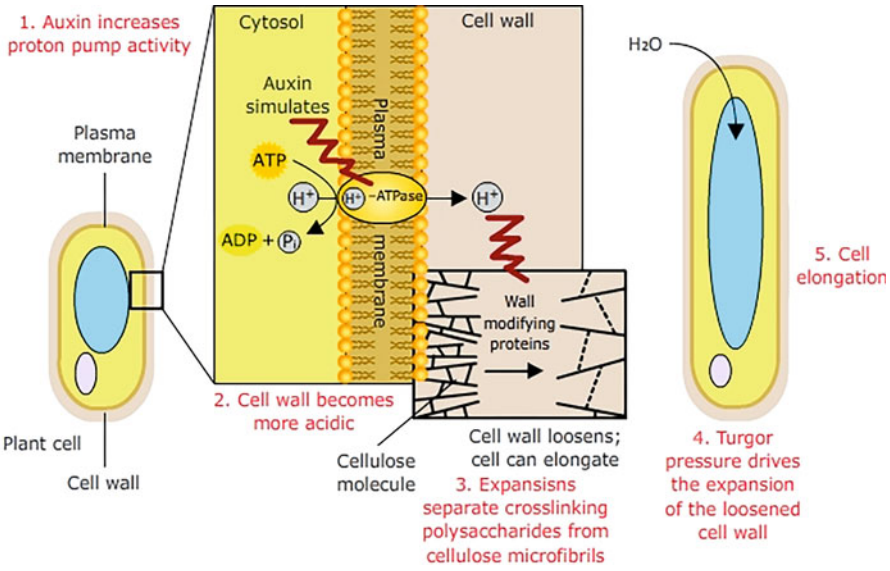


Fig. 24.12 Cell expansion is mediated by auxin-stimulated proton pump, which reduces the pH and promotes the activity of wall-loosening enzymes leading to loosening of cross-linking interactions of glycans with cellulose microfibrils

diffuse growth is affected by changes in the orientation of cellulose microfibrils in the cell wall in response to developmental and environmental cues. The tip growth mode of cell expansion is controlled by the dynamic cytoskeletal element F-actin that can change from single filaments and associate to from a dense meshwork forming a cytoskeletal array in the growing tips.

24.6.2 A Role for Cell Wall Components

The nature of cell wall varies between different cells and tissue types and is also a prerequisite for asymmetric divisions. Asymmetric division during pollen mitosis I is essential to the consequent differential expression of genes in the two daughter cells and is important for establishing the structurally and functionally different generative and vegetative cells. Similarly, in *Fucus* zygote asymmetric division leads to the formation of basal rhizoid and upper larger thallus cell with distinct fates. Evidences indicate the role of cell wall components such as sulfonated polysaccharides in determining the identities of the thallus and rhizoid cells by providing positional information. Recognition and localization of specific cell surface polysaccharide epitopes such as **arabinogalactans** (AGP) are possible using specific monoclonal antibodies. AGPs are differentially expressed during embryogenesis in *Brassica* highlighting cell differences between embryo proper and suspensor. The role of

cell wall components in establishing distinct fates during embryogenesis can be speculated by the observation that *GNOM* mutants that have a role in establishing the apical-basal patterning lack the GNOM protein that plays a role in protein trafficking and Golgi vesicle transport.

Summary

- Embryogenesis initiates with fertilization followed by regulated defined cell divisions to form a bilaterally asymmetric embryo.
- The apical-basal pattern with root and shoot polar axis and radial pattern having radially arranged layers of cells are established during embryogenesis.
- Several *Arabidopsis* mutants have been analyzed to identify genes that are related to the embryogenesis processes, which are important for organization of embryo. The mutants defective in normal apical-basal pattern formation include the *GNOM* that is linked to establishment of axial polarity and *MONOPTEROS* that is required for formation of the embryonic primary root as well as vascular development. These genes have been linked to the establishment of auxin-dependent signaling processes.
- Auxin functions as a chemical signal during embryogenesis. Discrete gradients of auxin are created during embryonic development through localized auxin synthesis and polar auxin transport.
- Polar auxin transport over long distances from the site of synthesis in apical tissues to the root tip regulates stem elongation, apical dominance, and lateral branching.
- Plant growth is limited to discrete regions called the meristems. Two such regions are the apical meristems located at the tips of roots and stems. These regions of active cell division are responsible for primary growth or the increase in the length of roots and stems.
- Plant cell growth is an irreversible change in cell size involving stretching of the cell wall driven by the internal turgor pressure of the cell walls.
- Cell growth appears to be initiated when these stresses are relaxed the activity of endogenous wall-loosening proteins, called expansins that characteristically weaken cross-links between cellulose molecules, increase wall extensibility, and allow for turgor-induced cell expansion.

Multiple-Choice Questions

1. Which of the following statements is **false** about the polarity of an embryo?
   (a) It is a term used to describe the differences along an axis such that one end of the axis is different from the other.
   (b) It is established only after the zygote divides.
   (c) It is important for development of structural axis of the body.
   (d) It is key to biological pattern formation.

2. The body plan of plant is distinguished by the _____pattern.
   (a) Apical, basal
   (b) Radial, apical
   (c) Apical-basal, radial
   (d) Apical-radial, basal
3. Growth and development of a plant body are the result of:
   (a) Differentiation
   (b) Cell division and enlargement
   (c) Morphogenesis
   (d) All of the above
4. Which of the following developmental mutants of *Arabidopsis* will lack both the apical and basal regions including the cotyledons and the root and so consist of a cellular mass with no obvious signs of apical-basal polarity?
   (a) *GNOM*
   (b) *GURKE*
   (c) *MONOPTEROS.*
   (d) *FACKEL*
5. The hormone that provides positional information for the coordination of correct cellular patterning from the globular stage onward:
   (a) Cytokinin
   (b) Gibberellin
   (c) Auxin
   (d) Ethylene
6. *SHR* (short root) and *SCR* (scarecrow) are involved in:
   (a) Ground tissue development
   (b) Apical-basal pattern
   (c) RAM development
   (d) Establishment of polarity
7. PIN-mediated auxin flow in the SAM directs auxin to:
   (a) Regions that flank SAM
   (b) Central zone
   (c) Rib zone
   (d) Leaf primordia
8. Antagonistic activity of the following two hormones in the basal cell is essential for normal development of RAM and enables the particular pattern of cell divisions that occur in the QC.
   (a) Cytokinin and gibberellin
   (b) Auxin and ethylene
   (c) Gibberellin and auxin
   (d) Cytokinin and auxin

9. Characteristic feature that distinguishes the development of a dicot embryo from a monocot embryo:
   (a) Asymmetric division of the zygote
   (b) Octant stage
   (c) Establishment of bilateral asymmetry
   (d) SAM is established at a lateral position opposite to the scutellum
10. The cell wall proteins that are activated by acidification and disrupt noncovalent binding between cellulose and hemicelluloses:
   (a) Cellulases
   (b) Hemicellulases
   (c) Expansins
   (d) Pectinases

Answers

1. b 2. c 3. d 4. a 5. c 6. a 7. a 8. d 9. d 10. c

Suggested Further Readings

Fosket DE (1994) Plant growth and development- a molecular approach. Academic, San Diego

Howell SH (1998) Molecular genetics of plant development. Cambridge University Press, Cambridge

Raghavan V (1997) Molecular embryology of flowering plants. Cambridge University Press, Cambridge