Chapter 35

Plant Structure, Growth, and Development

Lecture Outline

Overview

- A head of romanesco, an edible relative of broccoli, grows according to a repetitive program.
    - Romanesco is unusual in adhering so rigidly to its basic body organization.
- Most plants show much greater diversity in their individual forms.
    - This is because the growth of plants, more than animals, is affected by local environmental conditions.
    - All lions have four legs and are of roughly the same size, but oak trees will vary in the number and arrangement of their branches.
    - This is because lions respond to challenges and opportunities in their local environment by movement, whereas plants respond by altering their growth.
- Recognizing the highly adaptive development of plants is critical for understanding how plants interact with their environment.

Concept 35.1 Plants have a hierarchical organization consisting of organs, tissues, and cells.

- Plants, like multicellular animals, have organs that are composed of different tissues, and tissues that are composed of different cell types.
    - A **tissue** is a group of cells, consisting of one or more types, which perform a specific function.
    - An **organ** consists of several types of tissues that work together to carry out particular functions.

Vascular plants have three basic organs: roots, stems, and leaves.

- The basic morphology of vascular plants reflects their evolutionary history as terrestrial organisms that inhabit and draw resources from two very different environments.
    - Vascular plants obtain water and minerals from the soil.
    - Vascular plants obtain CO_2 and light above ground.
- To obtain the resources they need, vascular plants have evolved two systems: a subterranean **root system** and an aerial **shoot system** of stems and leaves.
- Each system depends on the other.
    - Lacking chloroplasts and living in the dark, roots would starve without *photosynthates*, the sugar and other carbohydrates imported from the shoot system.
    - Conversely, the shoot system depends on water and minerals that roots absorb from the soil.

Roots provide anchorage, absorption, and storage.

- A **root** is an organ that anchors a vascular plant in the soil, absorbs minerals and water, and often stores carbohydrates.
- Most eudicots and gymnosperms have a *taproot system*, consisting of one large vertical root (the **taproot**) that develops from an embryonic root.
  - The taproot produces many small **lateral roots**, also called branch roots.
  - Taproot systems generally penetrate deeply and are well adapted to deep soils.
- In most monocots, such as grasses, the embryonic root dies early and does not form a taproot.
  - Instead, many small roots grow from the stem. Such roots are *adventitious*, a terms describing a plant organ that grows in an unusual location.
- Each small root forms its own lateral roots, giving rise to a *fibrous root system*—a mat of thin roots that spread out below the soil surface.
  - A fibrous root system is usually shallower than a taproot system and is best adapted to shallow soils with light rainfall.
  - Grass roots are concentrated in the upper few centimeters of soil. As a result, grasses make excellent ground cover for preventing erosion.
- The root system helps anchor a plant.
- In both taproot and fibrous root systems, absorption of water and minerals occurs near the root tips, where vast numbers of tiny **root hairs** enormously increase the surface area.
  - Root hairs are thin, tubular extensions of individual root epidermal cells.
  - Despite their great surface area, root hairs contribute little to plant anchorage. Their main function is absorption.
- Many plants have root adaptations with specialized functions. Some arise from roots, while others are adventitious, arising above ground from stems or even from leaves.
  - Some modified roots provide additional support and anchorage.
  - Others store water and nutrients or absorb oxygen from the air.

Stems consist of alternating nodes and internodes.

- A **stem** is an organ that raises or separates leaves, exposing them to sunlight.
  - Stems also raise reproductive structures, facilitating dispersal of pollen and fruit.
- A stem consists of alternating **nodes**, the points at which leaves are attached, and **internodes**, the stem segments between nodes.
  - In the angle formed by each leaf and the stem is an **axillary bud** with the potential to form a lateral shoot or branch.
- The growth of a young shoot is usually concentrated at its apex, where there is an **apical bud**, or terminal bud, with developing leaves and a compact series of nodes and internodes.
- The presence of a terminal bud is partly responsible for inhibiting the growth of axillary buds, a phenomenon called **apical dominance**.
  - If the terminal bud is removed, the axillary buds break dormancy and give rise to lateral shoots complete with their own apical buds, leaves, and axillary buds.
  - This is why pruning trees and shrubs makes them bushier.
- Modified shoots with diverse functions (such as food storage and asexual reproduction) have evolved in many plants.

- These shoots, which include stolons, rhizomes, tubers, and bulbs, are often mistaken for roots.

Leaves are the main photosynthetic organs of most plants.

- The **leaf** is the primary site of photosynthetic organs in most plants, although green stems are also photosynthetic.
- Although leaves vary extensively in form, they generally consist of a flattened **blade** and a stalk, the **petiole**, which joins the leaf to a stem node.
  - Grasses and other monocots lack petioles. In these plants, the base of the leaf forms a sheath that envelops the stem.
- Monocots and eudicots differ in the arrangement of **veins**, the vascular tissue of leaves.
  - Most monocots have parallel major veins that run the length of the blade, while eudicot leaves have a branched network of major veins.
- Plant taxonomists use floral morphology, leaf morphology, the branching pattern of veins, and the spatial arrangement of leaves to help identify and classify plants.
  - For example, simple leaves have a single, undivided blade, while compound leaves have several leaflets attached to the petiole.
  - Many large leaves are compound, which allows them to withstand strong winds without tearing.
  - The structural adaptation of compound leaves also confines pathogens that invade the leaf to one leaflet.
- Almost all leaves are specialized for photosynthesis.
- Some plants have leaves that have become adapted for other functions, including tendrils that cling to supports, spines of cacti for defense, leaves modified for water storage, and brightly colored leaves that attract pollinators.

Plant organs are composed of three tissue systems: dermal, vascular, and ground.

- Each organ of a plant has three **tissue systems**: dermal, vascular, and ground tissues.
  - Each system is continuous throughout the plant body.
- The **dermal tissue system** is the plant's outer protective covering.
- In nonwoody plants, the dermal tissue system is a single layer of tightly packed cells, or **epidermis**.
- The epidermis of leaves and most stems secretes a waxy coating, the **cuticle**, which helps the aerial parts of the plant retain water.
- In woody plants, protective tissues called **periderm** replace the epidermis in older regions of stems and roots.
- The epidermis has other specialized characteristics consistent with the function of the organ it covers.
  - For example, the root hairs are extensions of epidermal cells near the tips of the roots.
  - *Trichomes* are outgrowths of shoot epidermis. In desert species, they reduce water loss, reflect light, and protect against insects by secreting sticky fluids or toxic compounds.
- The **vascular tissue system** is involved in the transport of materials between roots and shoots.
- The two types of vascular tissues are xylem and phloem.
  - **Xylem** conducts water and dissolved minerals upward from roots into the shoots.

- **Phloem** transports sugars, the products of photosynthesis, to the roots and sites of growth, such as developing leaves and fruits.

- The vascular tissue of a root or stem is called the **stele**.
  - In angiosperms, the root stele forms a solid central *vascular cylinder*, while the stele of stems and leaves consists of *vascular bundles*, separate strands of xylem and phloem.
  - Both xylem and phloem are complex tissues with a variety of cell types.
- The **ground tissue system** is tissue that is neither dermal nor vascular.
- Ground tissue is divided into **pith**, internal to vascular tissue, and **cortex**, external to the vascular tissue.
- The functions of specialized cells within ground tissue include photosynthesis, storage, and support.

Plant tissues are composed of three basic cell types: parenchyma, collenchyma, and sclerenchyma.

- Plant cells are differentiated, with each type of plant cell possessing structural adaptations that make specific functions possible.
  - Cell differentiation may be evident within the protoplast, the cell contents exclusive of the cell wall.
  - Modifications of cell walls also play a role in plant cell differentiation.
- The major types of differentiated plant cells are parenchyma, collenchyma, sclerenchyma, water-conducting cells of the xylem, and sugar-conducting cells of the phloem.
- Mature **parenchyma** cells have primary walls that are relatively thin and flexible; most lack secondary walls.
  - The protoplast of a parenchyma cell usually has a large central vacuole.
- Parenchyma cells are often depicted as "typical" plant cells because they generally are the least specialized, but there are exceptions.
  - For example, the highly specialized sieve-tube elements of the phloem are parenchyma cells.
- Parenchyma cells perform most of the metabolic functions of the plant, synthesizing and storing various organic products.
  - For example, photosynthesis occurs within the chloroplasts of parenchyma cells in the leaf.
  - Some parenchyma cells in the stems and roots have colorless plastids that store starch.
  - The fleshy tissue of most fruit is composed of parenchyma cells.
- Most parenchyma cells retain the ability to divide and differentiate into other cell types under special conditions, such as the repair and replacement of organs after injury to the plant.
- In the laboratory, it is possible to regenerate an entire plant from a single parenchyma cell.
- **Collenchyma cells** have thicker primary walls than parenchyma cells, although the walls are unevenly thick.
- Grouped into strands or cylinders, collenchyma cells help support young parts of the plant shoot.
- Young stems and petioles often have strands of collenchyma just below the epidermis, providing support without restraining growth.

- Mature collenchyma cells are living and flexible and elongate with the stems and leaves they support.
- **Sclerenchyma cells** have thick secondary walls usually strengthened by lignin; they function as supporting elements of the plant.
- Sclerenchyma cells are much more rigid than collenchyma cells.
- Unlike parenchyma cells, sclerenchyma cells cannot elongate.
  - Sclerenchyma cells occur in plant regions that have stopped lengthening.
- Many sclerenchyma cells are dead at functional maturity, but they produce rigid secondary cells walls before the protoplast dies.
- In parts of the plant that are still elongating, secondary walls are deposited in a spiral or ring pattern, enabling the cell wall to stretch like a spring as the cell grows.
- Two types of sclerenchyma cells, **fibers** and **sclereids**, are specialized entirely for support.
- Fibers are long, slender, and tapered, and usually occur in groups.
  - Fibers from hemp are used for making rope, and fibers from flax are woven into linen.
- Sclereids are irregular in shape and shorter than fibers. They have very thick, lignified secondary walls.
  - Sclereids impart hardness to nutshells and seed coats and the gritty texture to pear fruits.
- The water-conducting elements of xylem, **tracheids** and **vessel elements**, are elongated cells that are dead at functional maturity.
  - The thickened cell walls remain as a nonliving conduit through which water can flow.
- Both tracheids and vessels have secondary walls interrupted by **pits**, thinner regions where only primary walls are present.
  - Water moves from cell to cell mainly through pits.
- Tracheids are long, thin cells with tapered ends.
- Because their secondary walls are hardened with lignin, tracheids function in support as well as transport.
- Vessel elements are generally wider, shorter, thinner-walled, and less tapered than tracheids.
- Vessel elements are aligned end to end, forming long micropipes or xylem vessels.
  - The ends are perforated, enabling water to flow freely.
- In the phloem, sucrose, other organic compounds, and some mineral ions move through tubes formed by chains of cells called **sieve-tube elements**.
- Sieve-tube elements are alive at functional maturity, although a sieve-tube element lacks a nucleus, ribosomes, and a distinct vacuole.
  - The end walls, the sieve plates, have pores that facilitate the flow of fluid between cells.
- Each sieve-tube element has a nonconducting nucleated companion cell, which is connected to the sieve-tube element by numerous plasmodesmata.
  - The nucleus and ribosomes of the companion cell serve both that cell and the adjacent sieve-tube element.
- In some plants, companion cells in leaves help load sugar into the sieve-tube elements, which transport the sugars to other parts of the plant.

Concept 35.2 Meristems generate cells for primary and secondary growth.

- Unlike growth of many animals, plant growth is not limited to an embryonic or juvenile period.
  - Most plants demonstrate **indeterminate growth**, growing as long as the plant lives.
  - At any given time, a typical plant has embryonic, developing, and mature organs.
- In contrast, most animals and certain plant organs, such as flowers, leaves, and thorns, undergo **determinate growth**, ceasing to grow after they reach a certain size.
- A plant is capable of indeterminate growth because it has perpetually undifferentiated tissues called **meristems**.
  - There are two main types: apical meristems and lateral meristems.
- **Apical meristems**, located at the tips of roots and in axillary buds of shoots, supply cells for the plant to grow in length.
  - This elongation, **primary growth,** enables roots to extend through the soil and shoots to increase their exposure to light and carbon dioxide.
  - In herbaceous plants, primary growth produces almost all of the plant body.
- Woody plants also show **secondary growth**, progressive thickening of roots and shoots where primary growth has ceased.
  - Secondary growth is produced by **lateral meristems**, cylinders of dividing cells that extend along the lengths of roots and shoots.
  - The **vascular cambium** adds layers of vascular tissue called secondary xylem and phloem.
  - The **cork cambium** replaces the epidermis with thicker, tougher periderm.
- The cells within meristems divide to generate additional cells. Some cells remain in the meristem, while others differentiate and are incorporated into the tissues and organs of the growing plant.
  - Cells that remain as sources of new cells are called *stem cells* or *initials*.
  - Cells that are displaced from the meristem, called *derivatives*, continue to divide until the cells they produce become specialized within mature tissues.
- At the tip of a winter twig of a deciduous tree is the dormant apical bud, enclosed by scales that protect its apical meristem.
  - In the spring, the bud sheds its scales and begins a new spurt of primary growth.
  - Along each growth segment, nodes are marked by scars left when leaves fell in the autumn.
  - Above each leaf scar is either an axillary bud or a branch twig.
  - Farther down the twig are whorls of scars left by the scales that enclosed the apical bud during the preceding winter.
  - Each spring and summer, as primary growth extends the shoot, secondary growth thickens the parts of the shoot that formed in earlier years.
- Although plants grow throughout their lives, they do die.
- *Annuals* complete their life cycle—from germination to flowering to seed production to death—in a single year or less.
  - Many wildflowers and important food crops, such as cereals and legumes, are annuals.
- The lives of *biennials* span two years, with flowering and fruiting in the second year.
  - Turnips are biennials that are harvested after the first year.

- Plants such as trees, shrubs, and some grasses that live many years are *perennials*.
  - Some buffalo grass of the North American plains has been growing for 10,000 years from seeds that sprouted at the end of the last ice age.

Concept 35.3 Primary growth lengthens roots and shoots.

- Primary growth arises directly from cells produced by apical meristems.
- In herbaceous plants, the entire plant consists of primary growth, whereas in woody plants, only the young, non-woody parts of the plant are primary growth.
- Apical meristems lengthen both roots and shoots. However, there are important differences in the primary growth of these two systems.

Roots show primary growth.

- The root tip is covered by a thimble-like **root cap**, which protects the meristem as the root pushes through the abrasive soil during primary growth.
  - The cap also secretes a polysaccharide slime that lubricates the soil around the growing root tip.
- Growth occurs just behind the root tip in three overlapping zones of cells at successive stages of primary growth.
  - These zones—the zone of cell division, the zone of elongation, and the zone of differentiation—grade together.
- The *zone of cell division* includes the root apical meristem and its derivatives.
  - New root cells are produced in this region, including the the root cap.
- The zone of cell division blends into the *zone of elongation,* where cells elongate, sometimes to more than ten times their original length.
  - It is this elongation of cells that is mainly responsible for pushing the root tip, including the meristem, into the soil.
  - The meristem sustains growth by continuously adding cells to the youngest end of the zone of elongation.
- In the *zone of differentiation,* cells complete differentiation and become distinct cell types.
- The primary growth of roots produces the epidermis, ground tissue, and vascular tissue.
- Water and minerals absorbed from the soil must enter the plant through the epidermis, a single layer of cells covering the root.
  - Root hairs greatly increase the surface area of the epidermis.
- In angiosperm roots, the stele is a a vascular cylinder with a solid core of xylem and phloem.
  - In eudicot roots, xylem radiates from the center like a star, with phloem developing between the arms of the xylem “star.”
  - In monocot roots, the vascular tissue consists of a central core of parenchyma surrounded by a ring of xylem and a ring of phloem.
- The ground tissue of roots consists of parenchyma cells that fill the cortex, the region between the vascular cylinder and the epidermis.
  - Cells within the ground tissue store carbohydrates and absorb water and minerals from the soil.

- The innermost layer of the cortex, the **endodermis**, is a cylinder one cell thick that forms a selective barrier between the cortex and the vascular cylinder.
- Lateral roots may sprout from the outermost layer of the vascular cylinder, the **pericycle**.
  - A lateral root pushes through the cortex and epidermis to emerge from the established root.

Shoots show primary growth.

- The apical meristem of a shoot is a dome-shaped mass of dividing cells at the shoot tip.
- Leaves develop from **leaf primordia** on the flanks of the apical meristem.
- Within a bud, young leaves are crowded close together because the internodes are very short.
  - Shoot elongation is due to the lengthening of internode cells below the shoot apex.
- Branching arises from the activation of axillary buds.
  - Within each axillary bud is a shoot apical meristem.
  - Its dormancy depends mainly on its proximity to an active apical bud.
- In some monocots, including grasses, meristematic activity occurs at the bases of stems and leaves.
  - These areas, called *intercalary meristems*, allow damaged leaves to regrow.
  - This explains why grass continues to grow after mowing and enables the plant to recover more effectively from damage incurred from grazing herbivores.

Stems have characteristic organization of tissues.

- The epidermis covers stems as part of the continuous dermal tissue system.
- Unlike its central position in a root, vascular tissue runs the length of a stem in strands called vascular bundles.
  - Because the vascular system of the stem is near the surface, lateral shoots develop from axillary bud meristems on the stem's surface without having to originate from deep within the main shoot.
- In most eudicots, the vascular bundles are arranged in a ring.
  - The vascular bundles have xylem adjacent to the pith and phloem adjacent to the cortex.
- In the stems of most monocots, the vascular bundles are scattered throughout the ground tissue rather than arranged in a ring.
- In both monocots and eudicots, the stem's ground tissue is mostly parenchyma.
- Many stems are strengthened by collenchyma cells just beneath the epidermis.
  - Sclerenchyma fiber cells also provide support.

Leaves have characteristic organization of tissues.

- The epidermal barrier of leaves is interrupted by pores called **stomata**, which allow gas exchange between the surrounding air and the photosynthetic cells inside a leaf.
  - The stomata are also the major avenues of evaporative water loss from the plant—a process called transpiration.
- Each stomatal pore is flanked by two specialized epidermal cells called **guard cells**.
  - The term *stoma* can refer to either the stomatal pore or the entire stomatal complex, the pore and two guard cells.

- The ground tissue of the leaf, the **mesophyll,** is sandwiched between the upper and lower epidermis.
  - The mesophyll consists mainly of parenchyma cells specialized for photosynthesis.
  - In many eudicots, a layer or more of columnar *palisade mesophyll* lies above *spongy mesophyll*.
- CO_2 and oxygen circulate through the labyrinth of air spaces around the irregularly spaced cells of the spongy mesophyll.
  - The air spaces are particularly large near stomata, where gas exchange with the outside air occurs.
- The vascular tissue of a leaf is continuous with the vascular tissue of the stem.
- Within a leaf, veins subdivide repeatedly and branch throughout the mesophyll.
  - The xylem brings water and minerals to the photosynthetic tissues, and the phloem carries sugars and other organic products to other parts of the plant.
  - The vascular infrastructure also functions to support and reinforce the shape of the leaf.
- Each vein is enclosed in a protective *bundle sheath* consisting of one or more layers of parenchyma.
  - Bundle-sheath cells are prominent in leaves that undergo C_4 photosynthesis.

Concept 35.4 Secondary growth increases the diameter of stems and roots in woody plants.

- Secondary growth, the growth in thickness produced by lateral meristems, occurs in stems and roots of woody plants, but rarely in leaves.
- Secondary growth consists of the tissues produced by the vascular cambium and cork cambium.
  - The vascular cambium adds secondary xylem (wood) and secondary phloem, increasing vascular flow and support for the shoot system.
  - The cork cambium produces a tough, thick covering consisting of wax-impregnated cells that protect the stem from water loss and invasion by insects, bacteria, and fungal spores.
- All gymnosperms and many eudicots undergo secondary growth, but it is rare in monocots.
- Primary and secondary growth occur simultaneously but in different regions.
  - As primary growth lengthens stems and roots in the younger regions of a plant, secondary growth thickens stems and roots in older regions where primary growth has stopped.

The vascular cambium forms successive layers of secondary xylem to its interior and secondary phloem to its exterior.

- The accumulation of secondary xylem and phloem over the years accounts for most of the increase in diameter of a woody plant.
- The vascular cambium is a cylinder of meristematic cells, often only one cell thick. It develops from parenchyma cells that retain the capacity to divide.
  - In a typical woody stem, the vascular cambium forms as a continuous cylinder outside the cortex and primary xylem and inside the pith and primary phloem.
  - In a typical woody root, the vascular cambium forms in segments between the primary phloem, the lobes of primary xylem, and the pericycle.
- Viewed in cross section, the vascular cambium appears as a ring of initials.

- As meristematic cells divide, they increase the circumference of the vascular cambium, adding secondary xylem to the inside of the cambium and secondary phloem to the outside.

- Some initials are elongated, with long axes parallel to the axis of the stem or root.
  - These initials produce cells such as tracheids, vessel elements, and fibers of the xylem.
  - They also produce sieve-tube elements, companion cells, axially-oriented parenchyma, and fibers of the phloem.
- Other initials are shorter, oriented perpendicular to the axis of the stem or root.
  - These initials produce *vascular rays* that transfer water and nutrients laterally within the woody stem, store carbohydrates, and aid in wound repair.
- As secondary growth continues over the years, layer upon layer of secondary xylem accumulate, producing the tissue we call wood.
- Wood consists mainly of tracheids, vessel elements (in angiosperms), and fibers.
  - These cells, dead at functional maturity, have thick, lignified walls that give wood its hardness and strength.
- The first tracheid and vessel cells formed in the spring (early or spring wood) have larger diameters and thinner walls than the cells produced in the summer (late or summer wood).
  - The structure of the early wood maximizes delivery of water to new, expanding leaves.
  - The thick-walled cells of later wood provide more physical support.
- In temperate regions, secondary growth in perennial plants ceases during the winter.
- This pattern of growth—cambium dormancy, early wood production, and late wood production—produces annual growth rings.
- *Dendrochronology* is the science of analyzing tree ring growth patterns.
  - Scientists can use ring patterns to identify weather patterns and study climate change.
- As a tree or woody shrub ages, the older layers of secondary xylem, known as *heartwood*, no longer transport water and minerals.
  - Heartwood contains resins and other compounds that protect the core of the tree from fungi and insects.
- The outer layers, known as *sapwood*, continue to transport xylem sap.
- Because each new layer of secondary xylem has a larger circumference, secondary growth enables the xylem to transport more sap each year, supplying more leaves.
- Only the youngest secondary phloem, closest to the vascular cambium, functions in sugar transport.
- The older secondary phloem dies and is sloughed off as part of the bark.

The cork cambium replaces the epidermis with thicker, tougher periderm.

- Early in secondary growth, the epidermis produced by primary growth splits, dries, and falls off the stem or root.
- The epidermis is replaced by two tissues produced by the first cork cambium, which arises in the outer cortex of stems and in the outer layer of the pericycle of roots.
- The first tissue, *phelloderm*, is a thin layer of parenchyma cells that forms to the interior of the cork cambium.
- The cork cambium also produces cork cells, which accumulate at the cambium's exterior.

- Waxy material called *suberin* deposited in the cell walls of cork cells before they die acts as a barrier against water loss, physical damage, and pathogens.
- A cork cambium and the tissues it produces make up a layer of periderm, a protective layer that replaces the epidermis.
    - Because cork cells have suberin and are compacted together, the periderm is impermeable to water and gases.
- In most plants, water and minerals are absorbed in the youngest parts of the roots.
    - The older parts of the roots anchor the plant and transport water and solutes between roots and shoots.
- In areas called **lenticels**, spaces develop between the cork cells of the periderm.
    - These areas, which often appear as horizontal slits on the trunk, facilitate gas exchange with the outside air.
- The thickening of a stem or root splits the first cork cambium, which loses its meristematic activity and differentiates into cork cells.
- A new cork cambium forms to the inside, resulting in a new layer of periderm.
- As this process continues, older layers of periderm are sloughed off.
    - This produces the cracked, peeling bark of many tree trunks.
- **Bark** is all tissues external to the vascular cambium, including secondary phloem (produced by the vascular cambium), the most recent periderm, and all the outer layers of periderm.

How is secondary growth regulated?

- Important insights into the evolution of secondary growth have been achieved by studying the herbaceous plant *Arabidopsis thaliana.*
- Researchers have found that some secondary growth is initiated in *Arabidopsis* stems by the addition of weights to the plant.
    - These findings suggest that weight carried by the stem is the cue for wood formation.
- Several key genes that regulate shoot apical meristems in *Arabidopsis* also regulate vascular cambium activity in the poplar, *Populus trichocarpa*, suggesting the occurrence of evolutionarily conserved processes in apical and lateral meristems.

Concept 35.5 Growth, morphogenesis, and cell differentiation produce the plant body.

- The specific series of changes by which cells form tissues, organs, and organisms is called **development**.
    - Development unfolds according to the genetic information that an organism inherits from its parents but is also influenced by the external environment.
- A single genotype may produce different phenotypes in different environments. For example, the aquatic plant called the fanwort (*Cabomba caroliniana*) forms two very different types of leaves depending upon whether the shoot apical meristem is submerged or not.
    - This ability to alter form in response to local environmental conditions is called *developmental plasticity*.
    - Examples of plasticity are common in plants and may help compensate for plants' inability to escape adverse conditions by moving.

- There are three overlapping processes in development: growth, morphogenesis, and cell differentiation.
    - **Growth** is an irreversible increase in size.
    - **Morphogenesis** is the process that gives a tissue, organ, or organism its shape and determines the positions of cell types.
    - **Cell differentiation** is the process by which cells with the same genes become different from one another.

Applying techniques of modern molecular biology to model organisms has revolutionized the study of plant development.

- *Arabidopsis thaliana* is a favored model organism of plant geneticists and molecular biologists for many reasons.
    - It is small: thousands of plants can be cultivated in a few square meters of lab space.
    - It has a short generation time, taking about six weeks for a seed to grow into a mature plant that produces more seeds. This rapid maturation enables biologists to conduct genetic cross experiments in a relatively short time frame.
    - One plant can produce over 5,000 seeds, another property that makes *Arabidopsis* useful for genetic analysis.
- In addition, the plant's genome makes it particularly well suited for analysis by modern molecular genetic methods.
    - The *Arabidopsis* genome includes about 27,000 protein-encoding genes (more than humans). It is among the smallest known in plants.
    - The plant has only five pairs of chromosomes, making it easy to locate specific genes.
    - *Arabidopsis* was the first plant to have its entire genome sequenced.
- *Arabidopsis* is easy to transform by introducing foreign DNA.
    - Biologists transform plants by infecting them with genetically altered varieties of the bacterium *Agrobacterium tumefaciens*.
- Studying the effect of a mutation in a particular gene often yields important information about the gene's normal function.
    - Because *Agrobacterium* inserts its transforming DNA randomly into the genome, the DNA may be inserted in the middle of a gene sequence. This insertion usually destroys the function of the disrupted gene, resulting in a "knock-out mutant."
- Large-scale projects using this technique are underway to determine the function of every gene in *Arabidopsis*.
    - By identifying each gene's function and tracking every biochemical pathway, researchers aim to establish blueprints for how plants develop, a major goal of systems biology.

The plane and symmetry of cell division are important in plant development.

- New cell walls form in a plane (direction) perpendicular to the main axis of cell expansion.
    - The precise plane of cell division, determined during late interphase, usually corresponds to the shortest path that will halve the volume of the parent cell.
- The first sign of this spatial orientation is rearrangement of the cytoskeleton.
    - Microtubules in the cytoplasm become concentrated into a ring called the *preprophase band*. The band disappears before metaphase but predicts the future plane of cell division.
- It has long been thought that the plane of cell division provides the foundation for the forms of plant organs, but studies of an internally disorganized maize mutant called the *tangled-1* mutant have led researchers to question that view.

- In wild-type maize plants, leaf cells divide either transversely (crosswise) or longitudinally relative to the axis of the parent cell.
- Transverse divisions are associated with leaf elongation, and longitudinal divisions are associated with leaf broadening.

- In *tangled-1* mutant leaves, transverse divisions are normal, but most longitudinal divisions are oriented abnormally, leading to cells that are crooked or curved.
  - These abnormal cell divisions do not affect leaf shape.
  - Mutant leaves grow more slowly than wild-type leaves, but their overall shapes remain normal, indicating that leaf shape does not depend solely on precise spatial control of cell division.
- The shape of the shoot apex in *Arabidopsis* depends not upon the *plane* of cell division but rather on microtubule-dependent mechanical stresses stemming from the "crowding" associated with cell proliferation and growth.
- The *symmetry* of cell division—the distribution of cytoplasm between daughter cells—is important in determining cell fate.
- Although chromosomes are allocated to daughter cells equally during mitosis, the cytoplasm may divide asymmetrically.
  - *Asymmetrical cell division*, in which one daughter cell receives more cytoplasm than the other during mitosis, usually signals a key event in development.
- For example, the formation of guard cells typically involves both an asymmetrical cell division and a change in the plane of cell division.
  - An epidermal cell divides asymmetrically, forming a large cell that remains an unspecialized epidermal cell and a small cell that becomes the guard cell "mother cell."
  - Guard cells form when this small mother cell divides in a plane perpendicular to the first cell division.
  - Thus, asymmetrical cell division generates cells with different fates—that is, cells that mature into different types.
- Asymmetrical cell divisions also play a role in the establishment of **polarity**, the condition of having structural or chemical differences at opposite ends of an organism.
  - Plants typically have an axis, with a root end and a shoot end.
  - Such polarity is most obvious in morphological differences, but it is also apparent in physiological properties, including the unidirectional movement of the hormone auxin and the emergence of adventitious roots and shoots from "cuttings."
- Adventitious roots form within the root end of a stem cutting, and adventitious shoots arise from the shoot end of a root cutting.
  - The first division of a plant zygote is normally asymmetrical, initiating polarization of the plant body into shoot and root.
- This polarity is difficult to reverse experimentally, so the proper establishment of axial polarity is a critical step in a plant's morphogenesis.
- In the *gnom* mutant of *Arabidopsis*, the establishment of polarity is defective.
  - The first cell division of the zygote is abnormal because it is symmetrical, and the resulting ball-shaped plant has neither roots nor leaves.

Cell expansion differs between plants and animals.

- Animal cells grow mainly by synthesizing protein-rich cytoplasm, a metabolically expensive process.

- Growing plant cells also produce additional protein-rich material in their cytoplasm, but water uptake typically accounts for about 90% of expansion.
  - Most of this water is packaged in the large central vacuole.
- Vacuolar sap is very dilute and nearly devoid of the energetically expensive macromolecules that are found in great abundance in the rest of the cytoplasm.
  - Large vacuoles are therefore a “cheap” way of filling space, enabling a plant to grow rapidly and economically.
  - Bamboo shoots, for instance, can elongate more than 2 m per week.
- Rapid extensibility of shoots and roots was an important evolutionary adaptation that increased their exposure to light and soil.
- Plant cells rarely expand equally in all directions. Their greatest expansion is usually oriented along the plant’s main axis.
  - For example, cells near the tip of the root may elongate up to 20 times their original length, with relatively little increase in width.
- The orientation of cellulose microfibrils in the innermost layers of the cell wall causes this differential growth.
  - The microfibrils do not stretch, so the cell expands mainly perpendicular to the main orientation of the microfibrils.
- As with the plane of cell division, microtubules play a key role in regulating the plane of cell expansion.
  - It is the orientation of microtubules in the cell’s outermost cytoplasm that determines the orientation of cellulose microfibrils, the basic structural units of the cell wall.

During morphogenesis, cells acquire different identities in an ordered spatial arrangement.

- The development of specific structures in specific locations is called **pattern formation**.
- Two types of explanations have been put forward concerning how the fate of plant cells is determined during pattern formation.
- Hypotheses based on *lineage-based mechanisms* propose that cell fate is determined early in development and that cells pass on this destiny to their progeny.
  - According to this view, the basic pattern of cell differentiation is mapped out according to the directions in which meristematic cells divide and expand.
- On the other hand, hypotheses based on *position-based mechanisms* propose that the cell’s final position in an emerging organ determines what kind of cell it will become.
  - In support of this view, experimental manipulations of cell positions by surgically destroying certain cells with lasers have demonstrated that a plant cell’s fate is established late in development and largely depends upon signaling from neighboring cells.
- In contrast, cell fate in animals is largely determined by lineage-dependent mechanisms involving transcription factors.
  - The homeotic (*Hox*) genes that encode such transcription factors are critical for the proper number and placement of embryonic structures, such as the legs and antennae, in the fruit fly *Drosophila*.
- Maize has a homolog of *Hox* genes called *KNOTTED-1*, but unlike its counterparts in the animal world, *KNOTTED-1* does not affect the proper number or placement of plant organs.
  - An unrelated class of transcription factors called *MADS-box* proteins plays that role in plants.

- *KNOTTED-1* is important in the development of leaf morphology, including the production of compound leaves.
    - If the *KNOTTED-1* gene is expressed in greater quantity than normal in the genome of tomato plants, the normally compound leaves become “super-compound”.

Cells of a developing organism synthesize different proteins and diverge in structure and function despite sharing a common genome.

- Cellular differentiation depends, to a large degree, on the control of gene expression—the regulation of transcription and translation, resulting in the production of specific proteins.
- However, the fate of a plant cell is determined by its final position in the developing organ, not by cell lineage.
    - If an undifferentiated cell is displaced, it will differentiate into a cell type appropriate to its new position.
- One aspect of plant cell interaction is the communication of positional information from one cell to another.
    - Evidence suggests that the activation or inactivation of specific genes involved in cellular differentiation depends largely on cell-to-cell communication.
- For example, two cell types are formed in the root epidermis of *Arabidopsis*: root hair cells and hairless epidermal cells.
    - Cell fate is associated with the position of the epidermal cells.
    - The immature epidermal cells that are in contact with two underlying cells of the root cortex differentiate into root hair cells, whereas the immature epidermal cells in contact with only one cortical cell differentiate into mature hairless cells.
- Differential expression of a homeotic gene called *GLABRA-2* is required for appropriate root hair distribution.
    - Researchers have demonstrated this by coupling the *GLABRA-2* gene to a “reporter gene” that causes every cell expressing *GLABRA-2* in the root to turn pale blue following a certain treatment.
    - The *GLABRA-2* gene is normally expressed only in epidermal cells that will not develop root hairs.
- Plants pass through developmental phases, developing from a juvenile phase to an adult vegetative phase to an adult reproductive phase.
    - In animals, these developmental changes take place throughout the entire organism, such as when a larva develops into an adult animal.
    - In contrast, plant developmental phases occur within a single region, the shoot apical meristem.
- Morphological changes that arise from transitions in shoot apical meristem activity are called **phase changes**.
- During the transition from a juvenile phase to an adult phase, the most obvious morphological changes typically occur in leaf size and shape.
    - Juvenile nodes and internodes retain their juvenile status even after the shoot continues to elongate and the shoot apical meristem has changed to the adult phase.
    - Any *new* leaves that develop on branches that emerge from axillary buds at juvenile nodes will also be juvenile, even though the apical meristem of the stem’s main axis may have been producing mature nodes for years.

Biologists have made great progress in explaining the genetic control of floral development.

- Flower formation involves a phase change from vegetative growth to reproductive growth.
    - This transition is triggered by a combination of environmental cues, such as day length, and internal signals, such as hormones.
- Unlike vegetative growth, which is indeterminate, floral growth is determinate: The production of a flower by a shoot apical meristem stops the primary growth of that shoot.
- The transition from vegetative growth to flowering is associated with the switching on of floral **meristem identity genes**.
    - The protein products of these genes are transcription factors that regulate the genes required for the conversion of the indeterminate vegetative meristems to determinate floral meristems.
- When a shoot apical meristem is induced to flower, the order of each primordium's emergence determines its development into a specific type of floral organ—a sepal, petal, stamen, or carpel.
    - These floral organs form four whorls that can be described roughly as concentric "circles" when viewed from above.
    - Sepals form the first (outermost) whorl; petals form the second; stamens form the third; and carpels form the fourth (innermost) whorl.
- Plant biologists have identified several **organ identity genes** belonging to the *MADS-box* family that encode transcription factors that regulate the development of this floral pattern.
- Positional information determines which organ identity genes are expressed in a particular floral organ primordium.
    - The result is the development of an emerging floral primordium into a specific floral organ.
- A mutation in a plant organ identity gene can cause abnormal floral development, such as petals growing in place of stamens.
    - By studying mutants with abnormal flowers, researchers have identified and cloned three classes of floral organ identity genes.
- The **ABC hypothesis** of flower formation proposes that three classes of genes direct the formation of the four types of floral organs. According to this hypothesis, each class of organ identity genes is switched on in two specific whorls of the floral meristem.
    - Normally, *A* genes are switched on in the two outer whorls (sepals and petals); *B* genes are switched on in the two middle whorls (petals and stamens); and *C* genes are switched on in the two inner whorls (stamens and carpels).
    - Sepals arise from those parts of the floral meristems in which only *A* genes are active; petals arise where *A* and *B* genes are active; stamens where *B* and *C* genes are active; and carpels where only *C* genes are active.
- The ABC hypothesis can account for the phenotypes of mutants lacking *A*, *B*, or *C* gene activity, with one addition: Where gene *A* activity is present, it inhibits *C*, and vice versa. If either *A* or *C* is missing, the other takes its place.
- By constructing such hypotheses and designing experiments to test them, researchers are tracing the genetic basis of plant development.