**PLANT STRUCTURE AND GROWTH**

# Introduction

* With about 250,000 known species, the angiosperms are by far the most diverse and widespread group of land plants.
* As primary producers, flowering plants are at the base of the food web of nearly every terrestrial ecosystem.
* Most land animals, including humans, depend on plants directly or indirectly for sustenance.

## A. The Plant Body

1. Both genes and environment affect plant structure

* A plant’s structure reflects interactions with the environment on two time scales.
* Over the long term, entire plant species have, by natural selection, accumulated morphological adaptations that enhance survival and reproductive success.
* For example, some desert plants have so reduced their leaves that the stem is actually the primary photosynthetic organ.
* This is a morphological adaptation that reduces water loss.
* Over the short term, individual plants, even more than individual animals, exhibit structural responses to their specific environments.
* For example, the submerged aquatic leaves of Cabomba are feathery, enhancing the surface area available for the uptake of bicarbonate ion (HCO3-), the form of CO2 in water.
* Leaves that extend above the surface form oval pads that aid in flotation.
* The architecture of a plant is a dynamic process, continuously shaped by the plant’s genetically directed growth pattern along with fine-tuning to the environment.
* Even faster than a plant’s structural responses to environmental changes are its physiological (functional) adjustments.
* Most plants are rarely exposed to severe drought and rely mainly on physiological adaptations to cope with drought stress.
* In the most common response, the plant produces a hormone that cause the stomata, the pores in the leaves through which most of the water is lost, to close.

2. Plants have three basic organs: roots, stems, and leaves

* The plant body is a hierarchy of structural levels, with emergent properties arising from the ordered arrangement and interactions of component parts.
* The plant body consists of organs that are composed of different tissues, and these tissues are teams of different cell types.
* Although all angiosperms have a number of features in common, two plants groups, the monocots and dicots, differ in many anatomical details.
* The basic morphology of plants reflects their evolutionary history as terrestrial organisms that must simultaneously inhabit and draw resources from two very different environments.
* Soil provides water and minerals, but air is the main source of CO2 and light does not penetrate far into soil.
* 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 the sugar and other organic nutrients imported from the photosynthetic tissues of the shoot system.
* Conversely, the shoot system (and its reproductive tissues, flowers) depends on water and minerals absorbed from the soil by the roots.
* Roots anchor the plant in the soil, absorb minerals and water, and store food.
* Monocots, including grasses, generally have **fibrous root** systems, consisting of a mat of thin roots that spread out below the soil surface.
* This extends the plant’s exposure to soil water and minerals and anchors it tenaciously to the ground.
* Many dicots have a **taproot** system, consisting of one large vertical root (the taproot) that produces many small lateral, or branch, roots.
* The taproots not only anchor the plant in the soil, but they often store food that supports flowering and fruit production later.
* Most absorption of water and minerals in both systems occurs near the root tips, where vast numbers of tiny **root hairs** increase the surface area enormously.
* Root hairs are extensions of individual epidermal cells on the root surface.
* Some plants have roots, **adventitious** roots, arising aboveground from stems or even from leaves.
* In some plants, including corn, these adventitious roots function as props that help support tall stems.
* Shoots consist of stems and leaves.
* Shoot systems may be vegetative (leaf bearing) or reproductive (flower bearing).
* A stem is an alternative system of **nodes**, the points at which leaves are attached, and **internodes**, the stem segments between nodes.
* At the angle formed by each leaf and the stem is an **axillary bud**, with the potential to form a vegetative branch.
* Growth of a young shoot is usually concentrated at its apex, where there is a **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**.
* By concentrating resources on growing taller, apical dominance increases the plant’s exposure to light.
* In the absence of a terminal bud, the axillary buds break dominance and gives rise to a vegetative branch complete with its own terminal bud, leaves, and axillary buds.
* Modified shoots with diverse functions have evolved in many plants.
* These shoots, which include stolons, rhizomes, tubers, and bulbs, are often mistaken for roots.
* Stolons, such as the “runners” of strawberry plants, grow on the surface and enable a plant to colonize large areas asexually when a parent plant fragments into many smaller offspring.
* Rhizomes, like those of ginger, are horizontal stems that grow underground.
* Tubers, including potatoes, are the swollen ends of rhizomes specialized for food storage.
* Bulbs, such as onions, are vertical, underground shoots consisting mostly of the swollen bases of leaves that store food.
* Leaves are the main photosynthetic organs of most plants, but green stems are also photosynthetic.
* While 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.
* In the absence of petioles, such as in grasses and many other monocots, the base of the leaf forms a sheath that envelops the stem.
* Most monocots have parallel major veins that run the length of the blade, while dicot leaves have a multibranched network of major veins.
* Plant taxonomists use leaf shape, spatial arrangement of leaves, and the pattern of veins 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.
* A compound leaf has a bud where its petiole attaches to the stem, not at the base of the leaflets.
* Some plants have leaves that have become adapted by evolution for other functions.
* This includes tendrils to cling to supports, spines of cacti for defense, leaves modified for water storage, and brightly colored leaves that attract pollinators.

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

* Each organ of a plant has three tissue systems: the dermal, vascular, and the ground.
* Each system is continuous throughout the plant body.
* The **dermal tissue**, or **epidermis**, is generally a single layer of tightly packed cells that covers and protects all young parts of the plant.
* 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.
* The epidermis of leaves and most stems secretes a waxy coating, the **cuticle**, that helps the aerial parts of the plant retain water.
* **Vascular tissue**, continuous throughout the plant, is involved in the transport of materials between roots and shoots.
* **Xylem** conveys water and dissolved minerals upward from roots into the shoots.
* **Phloem** transports food made in mature leaves to the roots and to nonphotosynthetic parts of the shoot system.
* The water-conducting elements of xylem, the **tracheids** and **vessel elements**, are elongated cells that are dead at *functional maturity*, when these cells are fully specialized for their function.
* The thickened cell walls form 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.
* Tracheids are long, thin cells with tapered ends.
* Water moves from cell to cell mainly through pits.
* 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, **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, **sieve-tube members**.
* These are alive at functional maturity, although they lack the nucleus, ribosomes, and a distinct vacuole.
* The end walls, the **sieve plates**, have pores that presumably facilitate the flow of fluid between cells.
* A nonconducting nucleated **companion cell**, connected to the sieve-tube member, may assist the sieve-tube cell.
* **Ground tissue** is tissue that is neither dermal tissue nor vascular tissue.
* In dicot stems, ground tissue is divided into **pith**, internal to vascular tissue, and **cortex**, external to the vascular tissue.
* The functions of ground tissue include photosynthesis, storage, and support.
* For example, the cortex of a dicot stem typically consists of both fleshy storage cells and thick-walled support cells.

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

* Each type of plant cell has structural adaptations that make specific functions possible.
* These distinguishing characteristics may be present in the **protoplast**, the cell contents exclusive of the cell wall.
* Modifications of cell walls are also important in how the specialized cells of a plant function.
* In contrast to animal cells, plant cells may have chloroplasts, the site of photosynthesis; a central vacuole containing a fluid called cell sap and bounded by the tonoplast; and a cell wall external to the cell membrane.
* The protoplasts of neighboring cells are generally connected by plasmodesmata, cytoplasmic channels that pass through pores in the walls.
* The endoplasmic reticulum is continuous through the plasmodesmata in structures called desmotubules.
* An adhesive layer, the middle lamella, cements together the cell walls of adjacent cells.
* The primary cell wall is secreted as the cell grows.
* Some cells have secondary walls which develop after a cell stops growing.
* Mature **parenchyma** cells have primary walls that are relatively thin and flexible, and most lack secondary walls.
* 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 members 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 cells in the stems and roots have colorless plastids that store starch.
* The fleshy tissue of most fruit is composed of parenchyma cells.
* Developing plant cells of all types are parenchyma cells before specializing further in structure and function.
* Mature, unspecialized parenchyma cells do not generally undergo cell division.
* Most retain the ability to divide and differentiate into other cell types under special conditions - during 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, though the walls are unevenly thickened.
* Grouped into strands or cylinders, collenchyma cells help support young parts of the plant shoot.
* Young cells and petioles often have a cylinder of collenchyma just below their surface, providing support without restraining growth.
* Functioning collenchyma cells are living and flexible and elongate with the stems and leaves they support.
* **Sclerenchyma cells** also function as supporting elements of the plant, with thick secondary walls usually strengthened by lignin.
* They are much more rigid than collenchyma cells.
* Unlike parenchyma cells, they cannot elongate and 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, the secondary walls are deposited in a spiral or ring pattern, enabling the cell wall to stretch like a spring as the cell grows.
* Vessel elements and tracheids in the xylem are sclerenchyma cells that function for both support and transport.
* Two other sclerenchyma cells, **fibers** and **sclereids**, are specialized entirely in support.
* Fibers are long, slender and tapered, and usually occur in groups.
* Those from hemp fibers are used for making rope and those from flax for weaving into linen.
* Sclereids, shorter than fibers and irregular in shape, impart the hardness to nutshells and seed coats and the gritty texture to pear fruits.
* A major difference between plants and most animals is that the growth and development of plants is not just limited to an embryonic or juvenile period, but occurs throughout the life of the plant.
* At any given instance, a typical plant consists of embryonic organs, developing organs, and mature organs.

## B. The Process of Plant Growth and Development

* A plant’s continuous growth and development depend on processes that shape organs and generate specific patterns of specialized cells and tissues within these organs.
* **Growth** is the irreversible increase in mass that results from cell division and cell expansion.
* **Development** is the sum of all the changes that progressively elaborate an organism’s body.

1. Meristems generate cells for new organs throughout the lifetime of a plant: an overview of plant growth

* Most plants demonstrate indeterminate growth, growing as long as the plant lives.
* In contrast, most animals and certain plant organs, such as flowers and leaves, undergo determinate growth, ceasing to grow after they reach a certain size.
* Indeterminate growth does not mean immortality.
* **Annual** plants complete their life cycle—from germination through flowering and seed production to death—in a single year or less.
* Many wildflowers and important food crops, such as cereals and legumes, are annuals.
* The life of a **biennial** plant spans two years.
* Often, there is an intervening cold period between the vegetative growth season and the flowering season.
* Plants that live many years, including trees, shrubs, and some grasses, are **perennials**.
* These often die not from old age, but from an infection or some environmental trauma.
* A plant is capable of indeterminate growth because it has perpetually embryonic tissues called **meristems** in its regions of growth.
* These cells divide to generate additional cells, some of which remain in the meristematic region while others become specialized and are incorporated into the tissues and organs of the growing plant.
* Cells that remain as wellsprings of new cells in the meristem are called initials.
* Those that are displaced from the meristem, derivatives, continue to divide for some time until the cells they produce begin to specialize within developing tissues.
* The pattern of plant growth depends on the location of meristems.
* **Apical meristems**, located at the tips of roots and in the buds of shoots, supply cells for the plant to grow in length.
* This elongation, **primary growth**, enables roots to ramify through the soil and shoots to extend their exposure to light and carbon dioxide.
* Woody plants also show **secondary growth**, progressive thickening of roots and shoots.
* Secondary growth is the product of **lateral meristems**, cylinders of dividing cells extending along the length of roots and shoots.
* One lateral meristem replaces the epidermis with bark and a second adds layers of vascular tissue.
* In woody plants, primary growth is restricted to the youngest parts of the plant - the tips of the roots and shoots.
* The lateral meristems develop in slightly older regions of the roots and shoots.
* Secondary growth adds girth to the organs.
* Each growing season, primary growth produces young extensions of roots and shoots, while secondary growth thickens and strengthens the older part of the plant.
* At the tip of a winter twig of a deciduous tree is the dormant terminal bud, enclosed by scales that protect its apical meristem.
* In the spring, the bud will shed its scales and begin a new spurt of primary growth.
* Along each growth segment, nodes are marked by scars left when leaves fell in 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 terminal bud during the previous winter.
* Each spring and summer, as the primary growth extends the shoot, secondary growth thickens the parts of the shoot that formed in previous years.

2. Primary growth: Apical meristems extend roots and shoots by giving rise to the primary plant body

* Primary growth produces the **primary plant body** - the parts of the root and shoot systems produced by apical meristems.
* An herbaceous plant and the youngest parts of a woody plant represent the primary plant body.
* The root tip is covered by a thimblelike **root cap**, which protects the meristem as the root pushes through the abrasive soil during primary growth.
* The cap also secretes a lubricating slime.
* Growth in length is concentrated near the root’s tip, where three zones of cells at successive stages of primary growth are located.
* These zones—the zone of cell division, the zone of elongation, and the zone of maturation—grade together.
* The **zone of cell division** includes the apical meristem and its derivatives, primary meristems.
* The apical meristem produces the cells of the primary meristems and also replaces cells of the root cap that are sloughed off.
* Near the middle is the **quiescent center**, cells that divide more slowly than other meristematic cells.
* These cells are relatively resistant to damage from radiation and toxic chemicals.
* They may act as a reserve that can restore the meristem if it becomes damaged.
* Just above the apical meristem, the products of its cell division form three concentric cylinders of cells that continue to divide for some time.
* These primary meristems—the **protoderm**, **procambium**, and **ground meristem**—will produce the three primary tissue systems of the root: dermal, vascular, and ground tissues.
* 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, ahead.
* The meristem sustains growth by continuously adding cells to the youngest end of the zone of elongation.
* In the **zone of maturation**, cells begin to specialize in structure and function.
* In this root region, the three tissue systems produced by primary growth complete their differentiation, their cells becoming functionally mature.
* Three primary meristems give rise to the three primary tissues of roots.
* The epidermis develops from the dermal tissues.
* The ground tissue produces the endodermis and cortex.
* The vascular tissue produces the stele, the pericycle, pith, xylem, and phloem.
* The protoderm, the outermost primary meristem, produces the single cell layer of the epidermis.
* Water and minerals absorbed by the plant must enter through the epidermis.
* Root hairs enhance absorption by greatly increasing the surface area.
* The procambium gives rise to the **stele**, which in roots is a central cylinder of vascular tissue where both xylem and phloem develop.
* In dicot roots, the stele is a cylinder made up almost entirely of differentiated phloem and xylem cells, while in monocot roots the central cells in the stele remain as undifferentiated parenchyma cells, sometimes called pith.
* In dicots, the xylem cells radiate from the center of the stele in two or more spokes with phloem developing in the wedges between spokes.
* In monocots, the pith of the stele is generally ringed by vascular tissue with alternating patterns of xylem and phloem.
* The ground tissue between the protoderm and procambium gives rise to the ground tissue system.
* These are mostly parenchyma cells between the stele and epidermis.
* They store food and are active in the uptake of minerals that enter the root with the soil solution.
* The innermost layer of the cortex, the **endodermis**, is a cylinder one cell thick that forms a boundary between the cortex and stele.
* An established root may sprout **lateral roots** from the outermost layer of stele, the **pericycle**.
* Located just inside the endodermis, the pericycle is a layer of cells that may become meristematic and begin dividing.
* Through mitosis in the pericycle, the lateral root elongates and pushes through the cortex until it emerges from the main root.
* The stele of the lateral root maintains its connection to the stele of the primary root.
* The apical meristem of a shoot is a dome-shaped mass of dividing cells at the terminal bud.
* It forms the primary meristems - protoderm, procambium and ground meristem.
* Leaves arise as leaf primordia on the flanks of the apical meristem.
* Axillary buds develop from islands of meristematic cells left by apical meristems at the leaf primordia base.
* Within a bud, leaf primordia are crowded close together because internodes are very short.
* Most elongation of the shoot occurs by growth in length of slightly older internodes below the shoot apex.
* This growth is due to cell division and cell elongation within the internode.
* In some plants, including grasses, internodes continue to elongate all along the length of the shoot over a prolonged period.
* These plants have meristematic regions, called intercalary meristems, at the base of each internode.
* Axillary buds have the potential to form branches of the shoot system at some later time.
* While lateral roots originate from deep in the main root, branches of the shoot system originate from axillary buds, at the surface of a main shoot.
* Because the vascular system of the stem is near the surface, branches can develop with connections to the vascular tissue without having to originate from deep within the main shoot.
* Unlike their central position in a root, the vascular tissue runs the length of a stem in strands called **vascular bundles**.
* At the transition zone, the stem’s vascular bundles converge as the root’s vascular cylinder.
* Each vascular bundle of the stem is surrounded by ground tissue.
* In most dicots, the vascular bundles are arranged in a ring, with pith on the inside and cortex outside the ring.
* The vascular bundles have their xylem facing the pith and their phloem facing the cortex.
* Thin rays of ground tissue between the vascular bundles connect the two parts of the ground tissue system, the pith and 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 dicots, the stem’s ground tissue is mostly parenchyma, but many stems are strengthened by collenchyma just beneath the epidermis.
* Fiber cells of sclerenchyma also help support stems.
* The leaf epidermis is composed of cells tightly locked together like pieces of a puzzle.
* The leaf epidermis is a first line of defense against physical damage and pathogenic organisms and the waxy cuticle is a barrier to water loss from the plant.
* The epidermal barrier is interrupted only by the **stomata**, tiny pores flanked by specialized epidermal cells called **guard cells**.
* Each stoma is a gap between a pair of guard cells.
* The stomata allow gas exchange between the surrounding air and the photosynthetic cells inside the leaf.
* They are also the major avenues of evaporative water loss from the plant - a process called transpiration.
* The ground tissue of the leaf, the **mesophyll**, is sandwiched between the upper and lower epidermis.
* It consists mainly of parenchyma cells equipped with chloroplasts and specialized for photosynthesis.
* In many dicots, a level or more of columnar palisade parenchyma lies over spongy parenchyma.
* Carbon dioxide and oxygen circulate through the labyrinth of air spaces around the irregularly spaced cells.
* 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 xylem and phloem of the stem.
* Leaf traces, branches of vascular bundles in the stem, pass through petioles and into leaves.
* 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 its sugars and other organic products to other parts of the plant.
* The vascular infrastructure also reinforces the shape of the leaf.

3. Secondary growth: Lateral meristems add girth by producing secondary vascular tissue and periderm

* The stems and roots, but not the leaves, of most dicots increase in girth by secondary growth.
* The **secondary plant body** consists of the tissues produced during this secondary growth in diameter.
* The **vascular cambium** acts as a meristem for the production of secondary xylem and secondary phloem.
* The **cork cambium** acts as a meristem for a tough, thick covering for stems and roots that replaces the epidermis.
* The vascular cambium is a cylinder of meristematic cells that forms secondary vascular tissue.
* The accumulation of this tissue over the years accounts for most of the increase in diameter of a woody plant.
* Secondary xylem forms to the interior and secondary phloem to the exterior of the vascular cambium.
* While elongation of the stem (primary growth) occurs at the apical meristem, increases in diameter (secondary growth) occur farther down the stem.
* In these regions, some parenchyma cells regain the capacity to divide, becoming meristematic.
* This meristem forms in a layer between the primary xylem and primary phloem of each vascular bundle and in the rays of ground tissue between the bundles.
* The meristematic bands make a continuous cylinder of dividing cells surrounding the primary xylem and pith of the stem.
* This ring of vascular cambium consists of regions of ray initials and fusiform initials.
* **Ray initials** produce radial files of parenchyma cells known as xylem rays and phloem rays that transfer water and nutrients laterally within the woody stem and in the storage of starch and other reserves.
* The tapered, elongated cells of the **fusiform initials** form secondary xylem to the inside of the vascular cambium and secondary phloem to the outside.
* As secondary growth continues over the years, layer upon layer of secondary xylem accumulates, 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.
* In temperate regions, secondary growth in perennial plants ceases during the winter.
* The first tracheids and vessels cells formed in the spring (early wood) have larger diameters and thinner walls than cells produced later in the summer (late 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.
* This pattern of growth—cambium dormancy, early wood production, and late wood production—produces annual growth rings.
* Early in secondary growth, the epidermis produced by primary growth splits, dries, and falls.
* It is replaced by new protective tissues produced by cork cambium, a meristematic cylinder that first forms in the outer cortex of the stem and later in secondary phloem.
* Cork cambium produces cork cells, which accumulate at the cambium’s exterior.
* Waxy material deposited in the cell walls of cork cells before they die acts as a barrier against water loss, physical damage, and pathogens.
* The cork plus the cork cambium forms the **periderm**, a protective layer that replaces the epidermis.
* In areas called **lenticels**, splits develop in the periderm because of higher local activity of the cork cambium.
* These areas within the trunk facilitate gas exchange with the outside air.
* **Bark** refers to all tissues external to the vascular cambium, including secondary phloem, cork cambium, and cork.
* While cork initially develops from specialization of cells from the cortex, this supply is eventually exhausted and new cork cambium then develops from parenchyma cells in the secondary phloem.
* Only the youngest secondary phloem, internal to the cork cambium, functions in sugar transport.
* Older secondary phloem dies and helps protect the stem until it is sloughed off as part of the bark during later seasons of secondary growth.
* After several years of secondary growth, several zones are visible in a stem.
* These include two zones of secondary xylem (heartwood and sapwood), the vascular cambium, living secondary phloem, cork cambium, and cork.
* The heartwood no longer conducts water but its lignified walls of its dead cells form a central column that supports the tree.
* These cells are clogged with resins and other compounds that help protect the core from fungi and wood-boring insects.
* The sapwood functions in the upward transport of water and minerals, called the xylem sap.
* Because each new layer of secondary xylem has a larger circumference, secondary growth enables the xylem to transport more sap each year, providing water and minerals to an increasing number of leaves.
* While the pattern of growth and differentiation among the primary and secondary tissues of a woody shoot appears complex, there is an orderly transition of tissues that develop from the initial apical meristem of the stem.
* Two lateral meristems, vascular cambium and cork cambium, produce secondary growth in roots.
* The vascular cambium develops within the stele and produces secondary xylem on its inside and secondary phloem on its outside.
* As the stele grows in diameter, the cortex and epidermis are split and shed.
* A cork cambium forms from the pericycle and produces periderm, which becomes the secondary dermal tissue.
* Because the periderm is impermeable to water, only the youngest parts of the root, produced by primary growth, absorb water and minerals from the soil.
* Older parts of roots, with secondary growth, function mainly to anchor the plant and to transport water and solutes between the younger roots and the shoot system.
* Over the years, as the roots become woodier, annual rings develop and tissues external to the vascular cambium form a thick, tough bark.
* Old stems and old roots are quite similar.

## C. Mechanisms of Plant Growth and Development

* During plant development, a single cell, the zygote, gives rise to a multicellular plant of particular form with functionally integrated cells, tissues, and organs.
* Plants have tremendous developmental plasticity.
* Its form, including height, branching patterns, and reproductive output, is greatly influenced by environmental factors.
* A broad range of morphologies can result from the same genotype as the plant undergoes three developmental processes: growth, morphogenesis, and differentiation.

1. Molecular biology is revolutionizing the study of plants

* New laboratory and field methods coupled with clever choices of experimental organisms have catalyzes a research explosion in plant biology.
* Much of this research has focused on *Arabidopsis thaliana*, a small weed in the mustard family.
* Thousands of small plants can be cultivated in a few square meters of lab space.
* With a generation time of about six weeks, it is an excellent model for genetic studies.
* The genome of *Arabidopsis*, among the tiniest of all known plants, was the first plant genome sequenced, taking six years to complete.
* *Arabidopsis* has a total of about 26,000 genes, with fewer than 15,000 different types of genes.
* The functions of only about 45% of the *Arabidopsis* genes are known.
* Now that the DNA sequence of *Arabidopsis* is known, plant biologists working to identify the functions of every gene and track every chemical pathway to establish a blueprint for how plants are built.
* One key task is to identify which cells are manufacturing which gene products and at what stages in the plant’s life.
* One day it may be possible to create a computer-generated “virtual plant” that will enable researchers to visualize which plant genes are activated in different parts of the plant during the entire course of development.

2. Growth, morphogenesis, and differentiation produce the plant body

* An increase in mass, or growth, during the life of a plant results from both cell division and cell expansion.
* The development of body form and organization, including recognizable tissues and organs is called **morphogenesis**.
* The specialization of cells with the same set of genetic instructions to produce a diversity of cell types is called **differentiation**.

3. Growth involves both cell division and cell expansion

* Cell division in meristems, by increasing cell number, increases the potential for growth.
* However, it is cell expansion that accounts for the actual increase in plant mass.
* Together, these processes contribute to plant form.
* The plane (direction) of cell division is an important determinant of plant form.
* If the planes of division by a single cell and its descendents are parallel to the plane of the first cell division, a single file of cells will be produced.
* If the planes of cell division of the descendent cells are random, an unorganized clump of cells will result.
* While mitosis results in a symmetrical redistribution of chromosomes between daughter cells, cytokinesis does not have to be symmetrical.
* **Asymmetrical cell division**, in which one cell receives more cytoplasm than the other, is common in plant cells and usually signals a key developmental event.
* For example, this is how guard cells form from an unspecialized epidermal cell.
* The plane in which a cell will divide is determined during late interphase.
* Microtubules in the outer cytoplasm become concentrated into a ring, the **preprophase band.**
* While this disappears before metaphase, its “imprint” consists of an ordered array of actin microfilaments.
* These hold and fix the orientation of the nucleus and direct the movement of the vesicles producing the cell plate.
* Cell expansion in animal cells is quite different from cell expansion in plant cells.
* Animal cells grow by synthesizing a protein-rich cytoplasm, a metabolically expensive process.
* While growing plant cells add some organic material to their cytoplasm, the addition of water, primarily to the large central vacuole, accounts for 90% of a plant cell’s expansion.
* This enables plants to grow economically and rapidly.
* Rapid expansion of shoots and roots increases the exposure to light and soil, an important evolutionary adaptation to the immobile lifestyle of plants.
* The greatest expansion of a plant cell is usually oriented along the main axis of the plant.
* The orientations of cellulose microfibrils in the innermost layers of the cell wall cause this differential growth, as the cell expands mainly perpendicular to the “grain” of the microfibrils.
* A rosette-shaped complex of enzymes built into the plasma membrane synthesizes the microfibrils.
* The pattern of microfibrils mirrors the orientation of microtubules just across the plasma membrane.
* These microtubules may confine the cellulose-producing enzymes to a specific direction along the membrane.
* As the microfibrils extend in these channels, they are locked in place by cross-linking to other microfibrils, determining the direction of cell expansion.
* Studies of *Arabidopsis* mutants have confirmed the importance of cortical microtubules in both cell division and expansion.
* For example, plants that are *fass* mutants are unusually squat and seem to align their division planes randomly.
* They lack the ordered cell files and layers normally present.
* *Fass* mutants develop into tiny adult plants with all their organs compressed longitudinally.
* The cortical microtubular organization of *fass* mutants is abnormal.
* Although the microtubules involved in chromosome movement and in cell plate deposition are normal, the preprophase bands do not form prior to mitosis.
* In interphase cells, the cortical microtubules are randomly positioned.
* Therefore, the cellulose microfibrils deposited in the cell wall cannot be arranged to determine the direction of the cell’s elongation.
* Cells with *fass* mutations expand in all directions equally and divide in a haphazard arrangement, leading to stout stature and disorganized tissues.

**4. Morphogenesis depends on pattern formation**

* Morphogenesis organizes dividing and expanding cells into multicellular arrangements such as tissues and organs.
* The development of specific structures in specific locations is called **pattern formation**.
* Pattern formation depends to a large extent on **positional information**, signals that indicate each cell’s location within an embryonic structure.
* Within a developing organ, each cell continues to detect positional information and responds by differentiating into a particular cell type.
* Developmental biologists are accumulating evidence that gradients of specific molecules, generally proteins, provide positional information.
* For example, a substance diffusing from a shoot’s apical meristem may “inform” the cells below of their distance from the shoot tip.
* A second chemical signal produced by the outermost cells may enable a cell to gauge their radial position.
* The idea of diffusible chemical signals is one of several alternative hypotheses to explain how an embryonic cell determines its location.
* One type of positional information is **polarity**, the identification of the root end and shoot end along a well-developed axis.
* This polarity results in morphological differences and physiological differences, and it impacts the emergence of adventitious roots and shoots from cuttings.
* Initial polarization into root and shoot ends is normally determined by asymmetrical division of the zygote.
* In the *gnom* mutant of *Arabidopsis*, the first division is symmetrical and the resulting ball-shaped plant has neither roots nor cotyledons.
* Other genes that regulate pattern formation and morphogenesis include the homeotic genes, that mediate many developmental events, such as organ initiation.
* For example, the protein product of the *KNOTTED-1* homeotic gene is important for the development of leaf morphology, including production of compound leaves.
* Overexpression of this gene causes the compound leaves of a tomato plant to become “supercompound.”

5. Cellular differentiation depends on the control of gene expression

* The diverse cell types of a plant, including guard cells, sieve-tube members, and xylem vessel elements, all descend from a common cell, the zygote, and share the same DNA.
* Cellular differentiation occurs continuously throughout a plant’s life, as meristems sustain indeterminate growth.
* Differentiation reflects the synthesis of different proteins in different types of cells.
* For example, in *Arabidopsis* two distinct cell types, root hair cells and hairless epidermal cells, may develop from immature epidermal cells.
* Those in contact with one underlying cortical cell differentiate into mature, hairless cells, while those in contact with two underlying cortical cells differentiate into root hair cells.
* The homeotic gene, *GLABRA-2*, is normally expressed only in hairless cells, but if it is rendered dysfunctional, *every* root epidermal cell develops a root hair.
* In spite of differentiation, the cloning of whole plants from somatic cells supports the conclusion that the genome of a differentiated cell remains intact and can “dedifferentiate” to give rise to the diverse cell types of a plant.
* Cellular differentiation depends, to a large extent, on the control of gene expression.
* Cells with the same genomes follow different developmental pathways because they selectively express certain genes at specific times during differentiation.

6. Clonal analysis of the shoot apex emphasizes the importance of a cell’s location in its developmental fate

* In the process of shaping a rudimentary organ, patterns of cell division and cell expansion affect the differentiation of cells by placing them in specific locations relative to other cells.
* Thus, positional information underlies all the processes of development: growth, morphogenesis, and differentiation.
* One approach to studying the relationship among these processes is clonal analysis, mapping the cell lineages (clones) derived from each cell in an apical meristem as organs develop.
* Researchers induce some change in a cell that tags it in some way such that it (and its descendents) can be distinguished from its neighbors.
* For example, a somatic mutation in an apical cell that prevents chlorophyll production will produce an “albino” cell.
* This cell and all its descendants will appear as a linear file of colorless cells running down the long axis of the green shoot.
* To some extent, the developmental fates of cells in the shoot apex are predictable.
* For example, almost all the cells derived from division of the outermost meristematic cells end up as part of the dermal tissue of leaves and stems.
* However, it is not possible to pinpoint precisely which cells of the meristem will give rise to specific tissues and organs because random changes in rates and planes of cell division can reorganize the meristem.
* For example, while the outermost cells usually divide in a plane perpendicular to the shoot tip, occasionally a cell at the surface divides in a plane parallel to this meristematic layer, placing one daughter cell among cells derived from different lineages.
* In plants, a cell’s developmental fate is determined not by its membership in a particular lineage but by its *final* position in an emerging organ.

**7. Phase changes mark major shifts in development**

* The meristem can lay down identical repeating patterns of stems and leaves, but the meristem can also change from one developmental phase to another during its history - a process called a **phase change**.
* One example of a phase change is the gradual transition in vegetative (leaf-producing) growth from a juvenile state to a mature state in some species.
* The most obvious sign of this phase change is a change in the morphology of the leaves produced.
* The leaves of juvenile versus mature shoot regions differ in shape and other features.
* Once the meristem has laid down the juvenile nodes and internodes, they retain that status even as the shoot continues to elongate and the meristem eventually changes to the mature phase.
* If axillary buds give rise to branches, those shoots reflect the developmental phase of the main shoot region from which they arise.
* Though the main shoot apex may have made the transition to the mature phase, an older region of the shoot will continue to give rise to branches bearing juvenile leaves if that shoot region was laid down when the main apex was still in the juvenile phase.
* A branch with juvenile leaves may actually be *older* than a branch with mature leaves.
* The juvenile-to-mature phase transition highlights a difference in the development of plants versus animals.
* In an animal, this transition occurs at the level of the entire organism—as when a larvae develops into an adult animal.
* In plants, phase changes during the history of apical meristems can result in juvenile and mature regions coexisting along the axis of each shoot.

8. Genes controlling transcription play key roles in a meristem’s change from a vegetative to a floral phase

* Another striking passage in plant development is the transition from a vegetative shoot tip to a floral meristem.
* This is triggered by a combination of environmental cues, such as day length, and internal signals, such as hormones.
* Unlike vegetative growth, which is self-renewing, the production of a flower by an apical meristem terminates primary growth of that shoot tip as the apical meristem develops into the flower’s organs.
* This transition is associated with the switching on of floral **meristem identity genes**.
* Their protein products are transcription factors that help activate the genes required for the development of the floral meristem.
* Once a shoot meristem is induced to flower, positional information commits each primordium arising from the flanks of the shoot tip to develop into a specific flower organ.
* **Organ identity genes** regulate positional information and function in the development of the floral pattern.
* Mutations lead to the substitution of one type of floral organ where another would normally form.
* Organ identity genes code for transcription factors.
* Positional information determines which organ identity genes are expressed in which particular floral-organ primordium.
* In *Arabidopsis*, three classes of organ identity genes interact to produce the spatial pattern of floral organs by inducing the expression of those genes responsible for building an organ of specific structure and function.