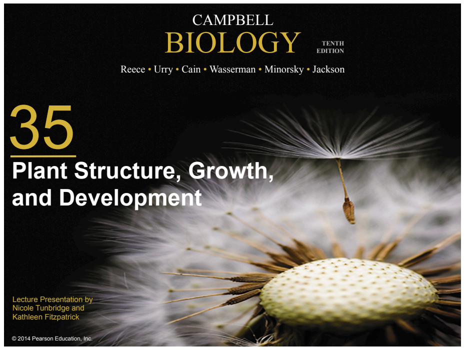


Are Plants Computers?

- Romanesco grows according to a repetitive program
- The development of plants depends on the environment and is highly adaptive
- Monocots and eudicots are the two major groups of angiosperms

Figure 35.1

Figure 35.1a

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

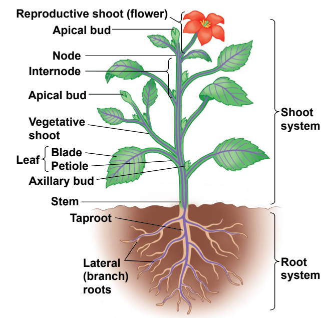
- Plants have organs composed of different tissues, which in turn are composed of different cell types
- An **organ** consists of several types of tissues that together carry out particular functions
- A **tissue** is a group of cells consisting of one or more cell types that together perform a specialized function

The Three Basic Plant Organs: Roots, Stems, and Leaves

- Basic morphology of vascular plants reflects their evolution as organisms that draw nutrients from below ground and above ground
- Plants take up water and minerals from below ground
- Plants take up CO_2 and light from above ground

- Three basic organs evolved: roots, stems, and leaves
- They are organized into a **root system** and a **shoot system**

Figure 35.2



- Roots rely on sugar produced by photosynthesis in the shoot system
- Shoots rely on water and minerals absorbed by the root system

Roots

- A **root** is an organ with important functions
  - Anchoring the plant
  - Absorbing minerals and water
  - Storing carbohydrates
- The primary root is the first root to emerge
- The primary root branches to form **lateral roots**, which improve anchorage and water absorption

- Tall plants with large shoot masses have a taproot system
- The **taproot** develops from the primary root and prevents the plant from toppling; lateral roots are responsible for absorption
- Small or trailing plants generally have a fibrous root system, which consists of
  - Adventitious roots that arise from stems or leaves
  - Lateral roots that arise from the adventitious roots

- In most plants, absorption of water and minerals occurs near the tips of roots
- **Root hairs** near the root tip increase the surface area of the root

Figure 35.3

- Many plants have root adaptations with specialized functions

Figure 35.4

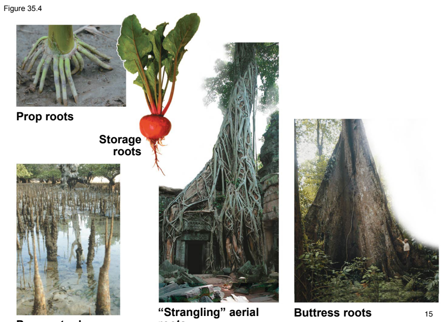


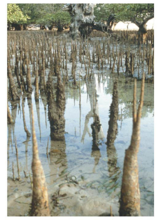
Figure 35.4a

Prop roots

Figure 35.4b

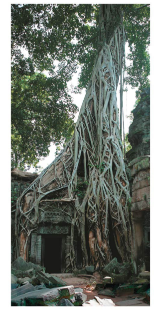
Storage roots

Figure 35.4c



Pneumatophores

Figure 35.4d



"Strangling" aerial roots

Figure 35.4e

Buttress roots

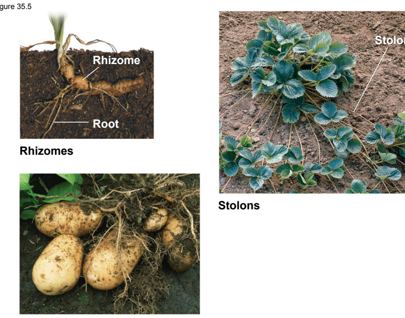
Stems

- A **stem** is an organ consisting of
  - An alternating system of **nodes**, the points at which leaves are attached
  - **Internodes**, the stem segments between nodes

- The growing shoot tip, or **apical bud**, causes elongation of a young shoot
- An **axillary bud** is a structure that has the potential to form a lateral branch, thorn, or flower

- Many plants have modified stems (e.g., rhizomes, stolons, tubers)

Figure 35.5

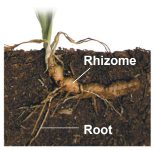


Rhizomes

Stolons

Tubers

Figure 35.5a



Rhizomes

Figure 35.5b

Stolons

Figure 35.5c

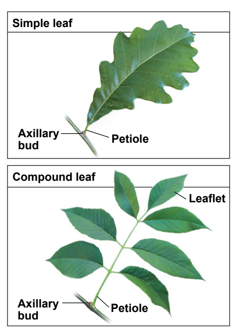
Tubers

Leaves

- The **leaf** is the main photosynthetic organ of most vascular plants
- Leaves intercept light, exchange gases, dissipate heat, and defend the plant from herbivores and pathogens
- Leaves generally consist of a flattened **blade** and a stalk called the **petiole**, which joins the leaf to a node of the stem

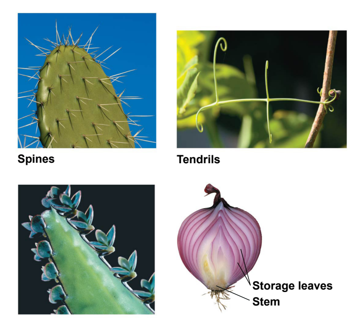
- Monocots and eudicots differ in the arrangement of **veins**, the vascular tissue of leaves
  - Most monocots have parallel veins
  - Most eudicots have branching veins
- In classifying angiosperms, taxonomists may use leaf morphology as a criterion

Figure 35.6



- Some plant species have evolved modified leaves that serve various functions

Figure 35.7



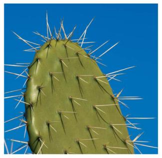
Spines

Tendrils

Reproductive leaves

Storage leaves

Figure 35.7a



Spines

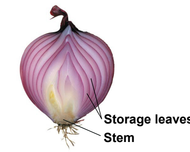
Figure 35.7b

Tendrils

Figure 35.7c

Reproductive leaves

Figure 35.7d

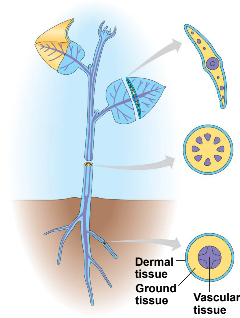


Storage leaves

Dermal, Vascular, and Ground Tissue Systems

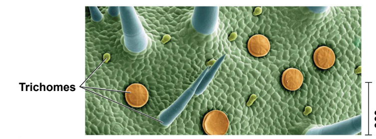
- Each plant organ has dermal, vascular, and ground tissues
- Each of these three categories forms a **tissue system**
- Each tissue system is continuous throughout the plant

Figure 35.8



- In nonwoody plants, the **dermal tissue system** consists of the **epidermis**
- A waxy coating called the **cuticle** helps prevent water loss from the epidermis
- In woody plants, protective tissues called **periderm** replace the epidermis in older regions of stems and roots
- Trichomes are outgrowths of the shoot epidermis and can help with reducing water loss and insect defense

Figure 35.9



- The **vascular tissue system** facilitates the transport of materials through the plant and provides mechanical support
- The two vascular tissues are xylem and phloem
- **Xylem** conducts water and dissolved minerals upward from roots into the shoots
- **Phloem** transports sugars from where they are made to where they are needed

- The vascular tissue of a root or stem is collectively called the **stele**
- In angiosperms the stele of the root is a solid central vascular cylinder
- The stele of stems and leaves is divided into vascular bundles, strands of xylem and phloem

- Tissues that are neither dermal nor vascular are the **ground tissue system**
- Ground tissue internal to the vascular tissue is **pith**; ground tissue external to the vascular tissue is **cortex**
- Ground tissue includes cells specialized for storage, photosynthesis, support, and transport

Common Types of Plant Cells

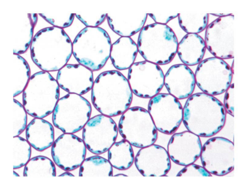
- As in any multicellular organism, a plant is characterized by cellular differentiation, the specialization of cells in structure and function

- The major types of plant cells are
  - Parenchyma
  - Collenchyma
  - Sclerenchyma
  - Water-conducting cells of the xylem
  - Sugar-conducting cells of the phloem

Parenchyma Cells

- Mature **parenchyma cells**
  - Have thin and flexible primary walls
  - Lack secondary walls
  - Are the least specialized
  - Perform the most metabolic functions
  - Retain the ability to divide and differentiate

Figure 35.10a

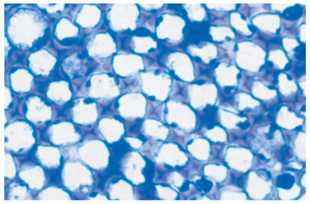


Parenchyma cells in a privet (*Ligustrum*) leaf (LM)

Collenchyma Cells

- **Collenchyma cells** are grouped in strands and help support young parts of the plant shoot
- They have thicker and uneven cell walls
- These cells provide flexible support without restraining growth

Figure 35.10b



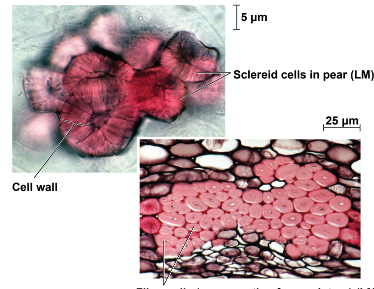
Collenchyma cells
(in *Helianthus* stem) (LM)

5 µm

Sclerenchyma Cells

- **Sclerenchyma cells** are rigid because of thick secondary walls strengthened with **lignin**, an indigestible strengthening polymer
- They are dead at functional maturity
- There are two types
  - **Sclereids** are short and irregular in shape and have thick lignified secondary walls
  - **Fibers** are long and slender and arranged in threads

Figure 35.10c



Fiber cells (cross section from ash tree) (LM)

Figure 35.10ca

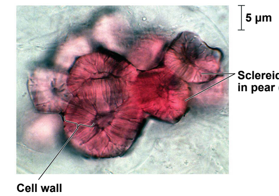
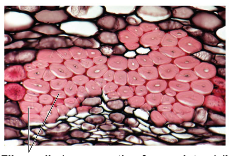


Figure 35.10cb

25 µm



Fiber cells (cross section from ash tree) (LM)

Water-Conducting Cells of the Xylem

- The two types of water-conducting cells, **tracheids** and **vessel elements**, are dead at maturity
- Tracheids are found in the xylem of all vascular plants

Figure 35.10d

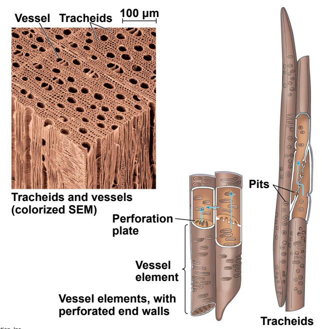
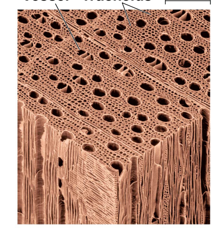


Figure 35.10da

Vessel Tracheids 100 µm



Tracheids and vessels
(colorized SEM)

- Vessel elements are common to most angiosperms and a few gymnosperms
- Vessel elements align end to end to form long micropipes called **vessels**

Sugar-Conducting Cells of the Phloem

- **Sieve-tube elements** are alive at functional maturity, though they lack organelles
- **Sieve plates** are the porous end walls that allow fluid to flow between cells along the sieve tube
- Each sieve-tube element has a **companion cell** whose nucleus and ribosomes serve both cells

Figure 35.10e

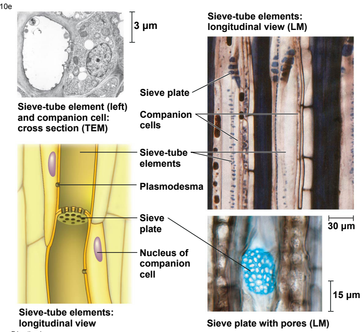
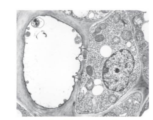


Figure 35.10ea



3 µm

Sieve-tube element (left)
and companion cell:
cross section (TEM)

Figure 35.10eb

Sieve-tube elements:
longitudinal view (LM)

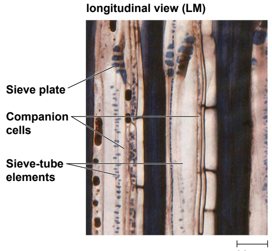
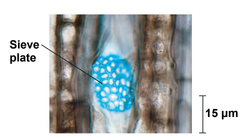
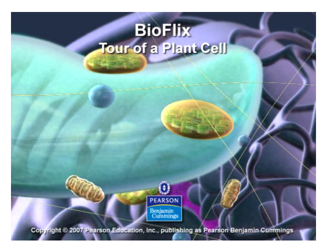


Figure 35.10ec



Sieve plate with pores (LM)

BioFlix: Tour of a Plant Cell



Concept 35.2: Different meristems generate new cells for primary and secondary growth

- A plant can grow throughout its life; this is called **indeterminate growth**
- **Meristems** are perpetually embryonic tissue and allow for indeterminate growth
- Some plant organs cease to grow at a certain size; this is called **determinate growth**

- There are two main types of meristems: apical meristems and lateral meristems
- **Apical meristems** are located at the tips of roots and shoots
- Apical meristems elongate shoots and roots, a process called **primary growth**

- **Lateral meristems** add thickness to woody plants, a process called **secondary growth**
- There are two lateral meristems: the vascular cambium and the cork cambium
- The **vascular cambium** adds layers of vascular tissue called secondary xylem (wood) and secondary phloem
- The **cork cambium** replaces the epidermis with periderm, which is thicker and tougher

Figure 35.11

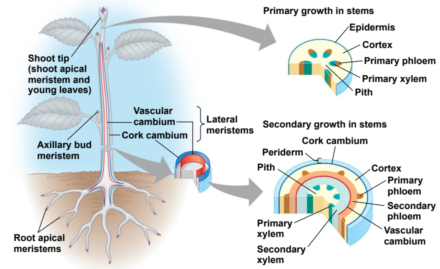


Figure 35.11a

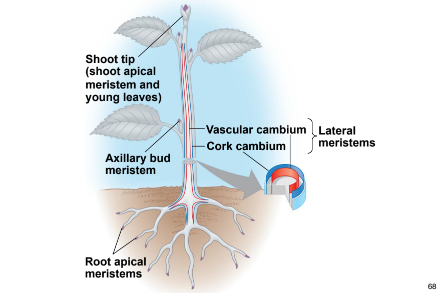
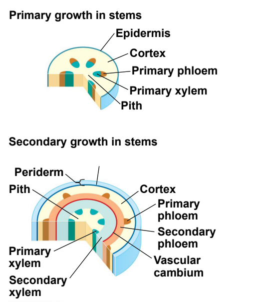
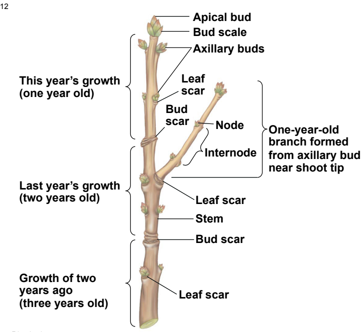


Figure 35.11b



- Meristems give rise to
  - Initials, also called stem cells, which remain in the meristem
  - Derivatives, which become specialized in mature tissues
- In woody plants, primary growth and secondary growth occur simultaneously but in different locations

Figure 35.12



- Flowering plants can be categorized based on the length of their life cycle
  - Annuals complete their life cycle in a year or less
  - Biennials require two growing seasons
  - Perennials live for many years

Concept 35.3: Primary growth lengthens roots and shoots

- Primary growth arises from cells produced by apical meristems and elongates parts of the root and shoot systems

Primary Growth of Roots

- The root tip is covered by a **root cap**, which protects the apical meristem as the root pushes through soil
- Growth occurs just behind the root tip, in three zones of cells
  - Zone of cell division
  - Zone of elongation
  - Zone of differentiation, or maturation

Figure 35.13

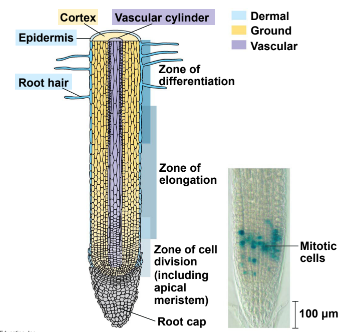
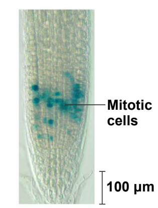
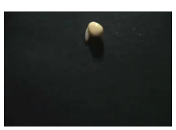


Figure 35.13a



Video: Root Growth in a Radish Seed (Time Lapse)



- The primary growth of roots produces the epidermis, ground tissue, and vascular tissue
- In angiosperm roots, the stele is a vascular cylinder
- In most eudicots, the xylem is starlike in appearance with phloem between the "arms"
- In many monocots, a core of parenchyma cells is surrounded by rings of xylem then phloem

Figure 35.14

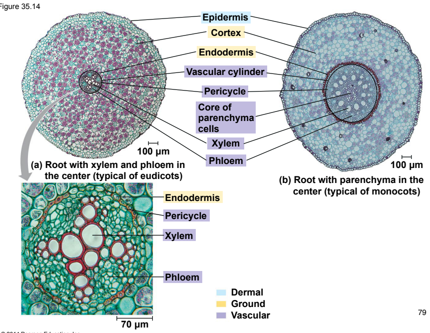


Figure 35.14a

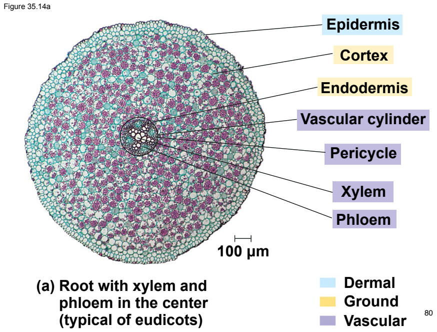
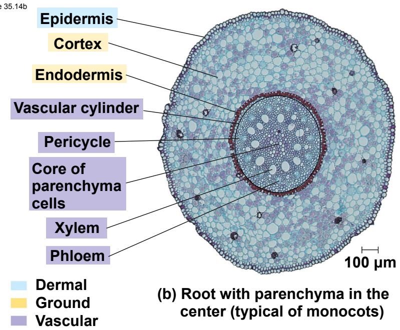
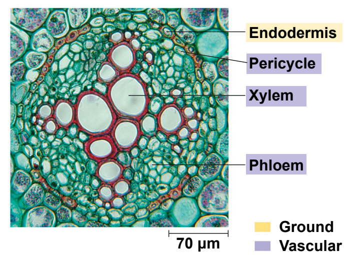


Figure 35.14b



(b) Root with parenchyma in the center (typical of monocots)

Figure 35.14c



- The ground tissue, mostly parenchyma cells, fills the cortex, the region between the vascular cylinder and epidermis
- The innermost layer of the cortex is called the **endodermis**
- The endodermis regulates passage of substances from the soil into the vascular cylinder

- Lateral roots arise from within the **pericycle**, the outermost cell layer in the vascular cylinder

Figure 35.15-1

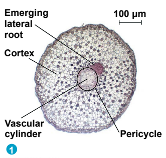


Figure 35.15-2

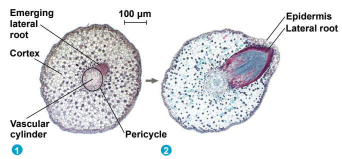


Figure 35.15-3

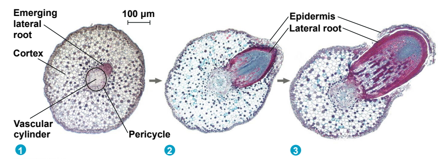


Figure 35.15a

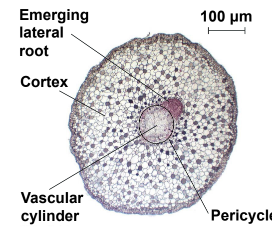


Figure 35.15b

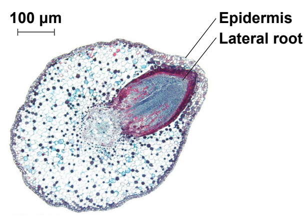
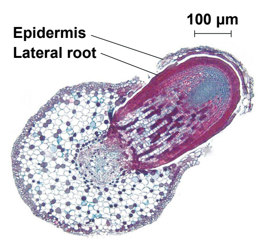


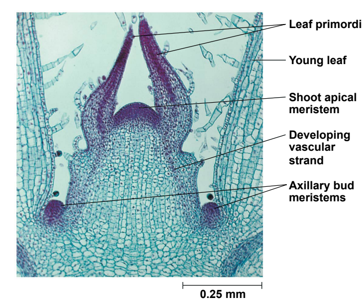
Figure 35.15c



Primary Growth of Shoots

- A shoot apical meristem is a dome-shaped mass of dividing cells at the shoot tip
- Leaves develop from **leaf primordia** along the sides of the apical meristem
- Axillary buds develop from meristematic cells left at the bases of leaf primordia

Figure 35.16

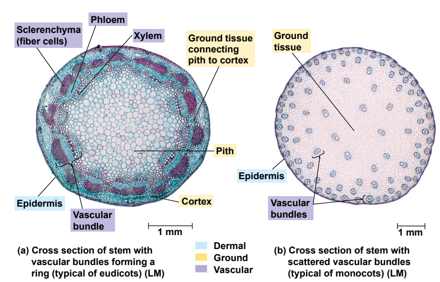


- The closer an axillary bud is to the active apical bud, the more inhibited it is
- Axillary buds are released from this **apical dominance** if the shoot tip is removed or shaded
- In some monocots, meristematic activity occurs at the bases of stems and leaves

Tissue Organization of Stems

- Lateral shoots develop from axillary buds on the stem's surface
- In most eudicots, the vascular tissue consists of vascular bundles arranged in a ring

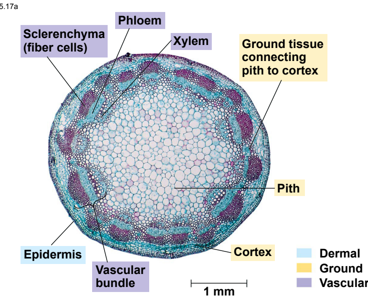
Figure 35.17



(a) Cross section of stem with vascular bundles forming a ring (typical of eudicots) (LM)

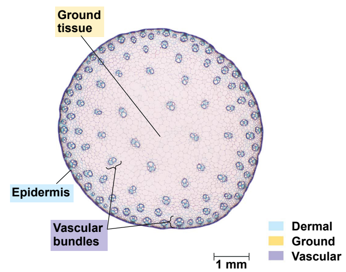
(b) Cross section of stem with scattered vascular bundles (typical of monocots) (LM)

Figure 35.17a



(a) Cross section of stem with vascular bundle forming a ring (typical of eudicots) (LM)

Figure 35.17b



(b) Cross section of stem with scattered vascular bundles (typical of monocots) (LM)

- In most monocot stems, the vascular bundles are scattered throughout the ground tissue, rather than forming a ring

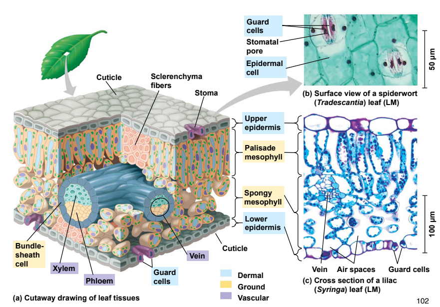
Tissue Organization of Leaves

- The epidermis in leaves is interrupted by **stomata**, pores that allow CO_2 and O_2 exchange between the air and the photosynthetic cells in a leaf
- Stomata are also major avenues for evaporative loss of water
- Each stomatal pore is flanked by two **guard cells**, which regulate its opening and closing

- The ground tissue in a leaf, called **mesophyll**, is sandwiched between the upper and lower epidermis
- The mesophyll of eudicots has two layers
  - The palisade mesophyll in the upper part of the leaf
  - The spongy mesophyll in the lower part of the leaf; the loose arrangement allows for gas exchange

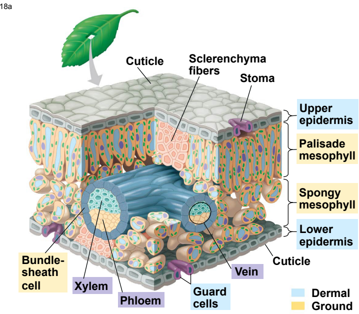
- The vascular tissue of each leaf is continuous with the vascular tissue of the stem
- Veins are the leaf's vascular bundles and function as the leaf's skeleton
- Each vein in a leaf is enclosed by a protective bundle sheath

Figure 35.18



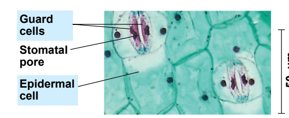
(a) Cutaway drawing of leaf tissues

Figure 35.18a



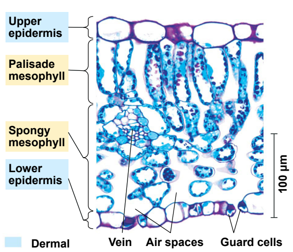
(a) Cutaway drawing of leaf tissues

Figure 35.18b



(b) Surface view of a spiderwort (*Tradescantia*) leaf (LM)

Figure 35.18c



(c) Cross section of a lilac (*Syringa*) leaf (LM)

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

- Many land plants display secondary growth, the growth in thickness produced by lateral meristems
- Secondary growth is characteristic of gymnosperms and many eudicots, but not monocots

- Secondary growth 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
- Primary growth and secondary growth occur simultaneously

Figure 35.19

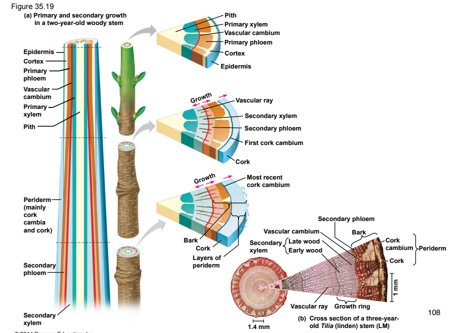


Figure 35.19a-1

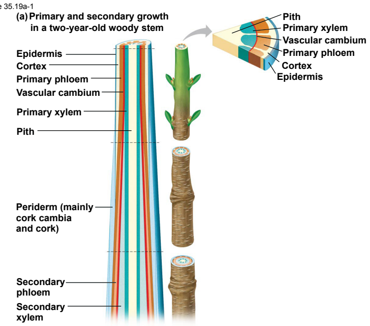


Figure 35.19a-2

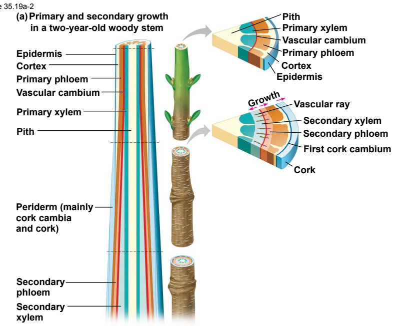


Figure 35.19a-3

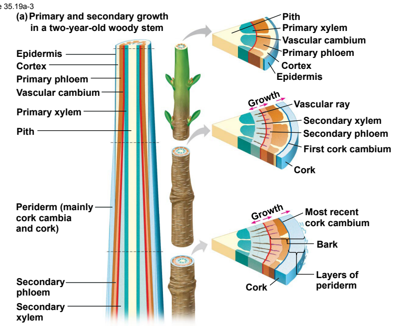
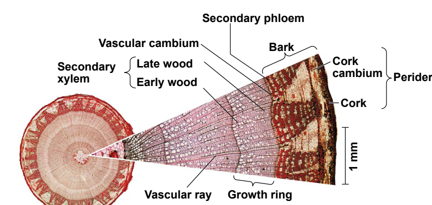


Figure 35.19b



(b) Cross section of a three-year-old *Tilia* (linden) stem (LM)

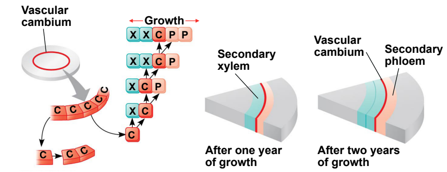
The Vascular Cambium and Secondary Vascular Tissue

- The vascular cambium, a cylinder of meristematic cells one cell layer thick, is wholly responsible for the production of secondary vascular tissue
- It develops from undifferentiated parenchyma cells

- In a typical woody stem, the vascular cambium is located outside the pith and primary xylem and to the inside of the primary phloem and the cortex
- In a typical woody root, the vascular cambium forms exterior to the primary xylem and interior to the primary phloem and pericycle

- In cross section, the vascular cambium appears as a ring of meristematic cells
- Division of these cells increases the vascular cambium's circumference and adds secondary xylem to the inside and secondary phloem to the outside

Figure 35.20

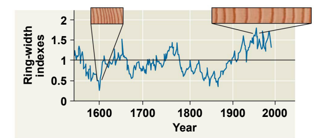


- Elongated initials produce tracheids, vessel elements, fibers of xylem, sieve-tube elements, companion cells, axially oriented parenchyma, and fibers of the phloem
- Shorter initials produce vascular rays, radial files of parenchyma cells that connect secondary xylem and phloem

- Secondary xylem accumulates as wood and consists of tracheids, vessel elements (only in angiosperms), and fibers
- Early wood, formed in the spring, has thin cell walls to maximize water delivery
- Late wood, formed in late summer, has thick-walled cells and contributes more to stem support

- Tree rings are visible where late and early wood meet, and can be used to estimate a tree's age
- Dendrochronology is the analysis of tree ring growth patterns and can be used to study past climate change

Figure 35.21



- As a tree or woody shrub ages, the older layers of secondary xylem, the heartwood, no longer transport water and minerals
- The outer layers, known as sapwood, still transport materials through the xylem
- Older secondary phloem sloughs off and does not accumulate

Figure 35.22

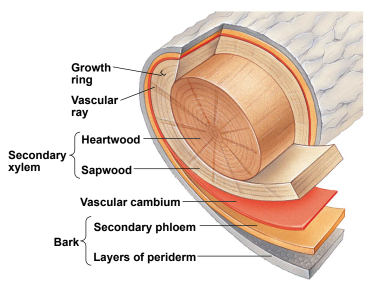
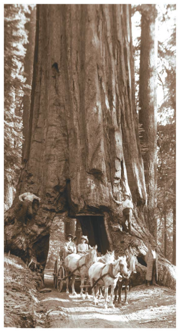


Figure 35.23



The Cork Cambium and the Production of Periderm

- Cork cambium gives rise to cork cells that accumulate to the exterior of the cork cambium
- Cork cells deposit waxy suberin in their walls, then die
- The cork cambium and the tissues it produces compose a layer of periderm

- **Lenticels** in the periderm allow for gas exchange between living stem or root cells and the outside air
- **Bark** consists of all the tissues external to the vascular cambium, including secondary phloem and periderm

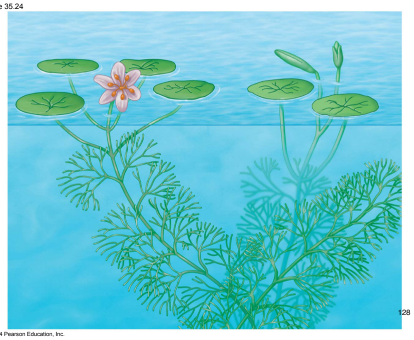
Evolution of Secondary Growth

- In the herbaceous plant *Arabidopsis*, the addition of weights to the plants triggered secondary growth
- This suggests that stem weight is the cue for wood formation

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

- Cells form specialized tissues, organs, and organisms through the process of **development**
- Developmental plasticity describes the effect of environment on development
  - For example, the aquatic plant fanwort forms different leaves depending on whether or not the apical meristem is submerged

Figure 35.24



- Development consists of growth, morphogenesis, and cell differentiation
- Growth is an irreversible increase in size
- Morphogenesis is the development of body form and organization
- Cell differentiation is the process by which cells with the same genes become different from each other

Model Organisms: Revolutionizing the Study of Plants

- New techniques and model organisms are catalyzing explosive progress in our understanding of plants
- *Arabidopsis* is a model organism and the first plant to have its entire genome sequenced
- *Arabidopsis* has 27,000 genes divided among five pairs of chromosomes

Figure 35.UN02

- *Arabidopsis* is easily transformed by introducing foreign DNA via genetically altered bacteria
- Studying the genes and biochemical pathways of *Arabidopsis* will provide insights into plant development, a major goal of systems biology

Figure 35.25-1

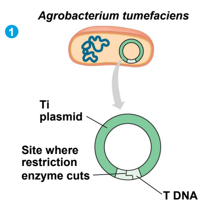


Figure 35.25-2

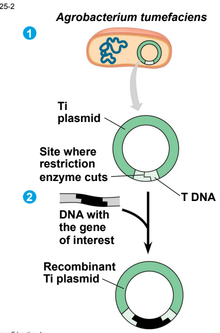


Figure 35.25-3

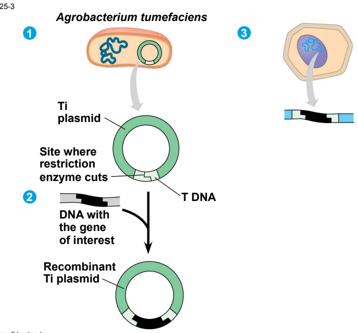
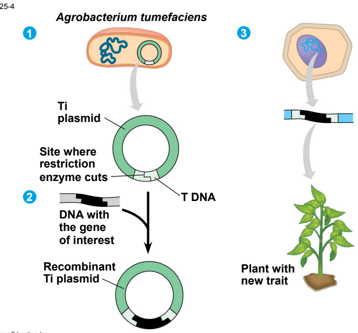


Figure 35.25-4



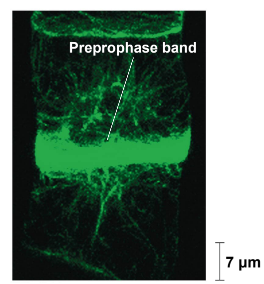
Growth: Cell Division and Cell Expansion

- By increasing cell number, cell division in meristems increases the potential for growth
- Cell enlargement accounts for the actual increase in plant size

The Plane and Symmetry of Cell Division

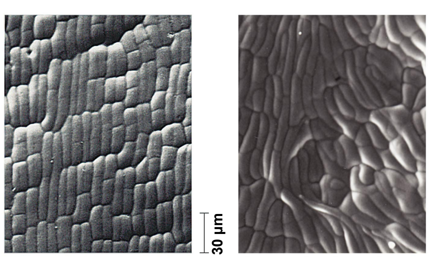
- New cell walls form in a plane (direction) perpendicular to the main axis of cell expansion
- The plane in which a cell divides is determined during late interphase
- Microtubules become concentrated into a ring called the preprophase band that predicts the future plane of cell division

Figure 35.26



- Leaf growth results from a combination of transverse and longitudinal cell divisions
- It was previously thought that the plane of cell division determines leaf form
- A mutation in the *tangled-1* gene that affects longitudinal divisions does not affect leaf shape

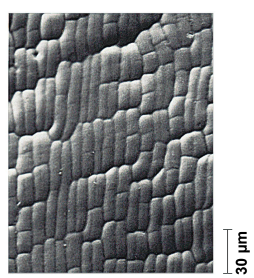
Figure 35.27



Leaf epidermal cells of wild-type maize

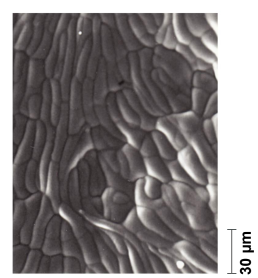
Leaf epidermal cells of *tangled-1* maize mutant

Figure 35.27a



Leaf epidermal cells of wild-type maize

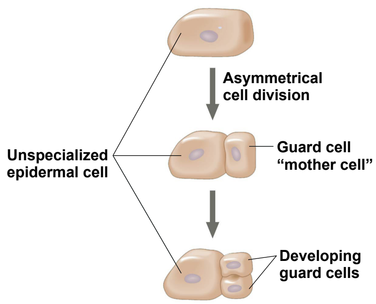
Figure 35.27b



Leaf epidermal cells of *tangled-1* maize mutant

- The symmetry of cell division, the distribution of cytoplasm between daughter cells, determines cell fate
- Asymmetrical cell division signals a key event in development
  - For example, the formation of guard cells involves asymmetrical cell division and a change in the plane of cell division

Figure 35.28



- **Polarity** is the condition of having structural or chemical differences at opposite ends of an organism
  - For example, plants have a root end and a shoot end
- Asymmetrical cell divisions play a role in establishing polarity

- The first division of a plant zygote is normally asymmetrical and initiates polarization into the shoot and root
- The *gnom* mutant of *Arabidopsis* results from a symmetrical first division

Figure 35.29

Orientation of Cell Expansion

- Plant cells grow rapidly and "cheaply" by intake and storage of water in vacuoles
- Plant cells expand primarily along the plant's main axis
- Cellulose microfibrils in the cell wall restrict the direction of cell elongation

Figure 35.30

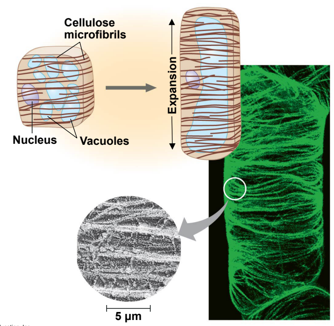


Figure 35.30a

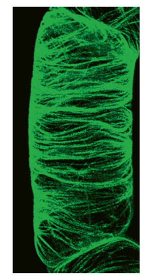
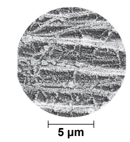


Figure 35.30b



Morphogenesis and Pattern Formation

- **Pattern formation** is the development of specific structures in specific locations
- Two types of hypotheses explain the fate of plant cells
  - Lineage-based mechanisms propose that cell fate is determined early in development and passed on to daughter cells
  - Position-based mechanisms propose that cell fate is determined by final position

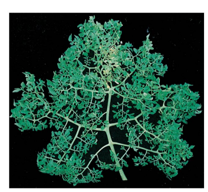
- Experiments suggest that plant cell fate is established late in development and depends on cell position
- In contrast, cell fate in animals is largely lineage dependent

- *Hox* genes in animals affect the number and placement of appendages in embryos
- A plant homolog of *Hox* genes called *KNOTTED-1* does not affect the number or placement of plant organs
- *KNOTTED-1* is important in the development of leaf morphology

Figure 35.31

Figure 35.31a

Figure 35.31b

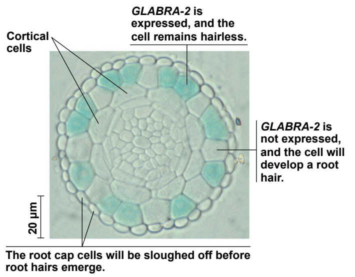


Gene Expression and the Control of Cell Differentiation

- Cells of a developing organism synthesize different proteins and diverge in structure and function even though they have a common genome
- Cellular differentiation depends on gene expression, but is determined by position
- Positional information is communicated through cell interactions

- Gene activation or inactivation depends on cell-to-cell communication
  - For example, *Arabidopsis* root epidermis forms root hairs or hairless cells depending on the number of cortical cells it is touching

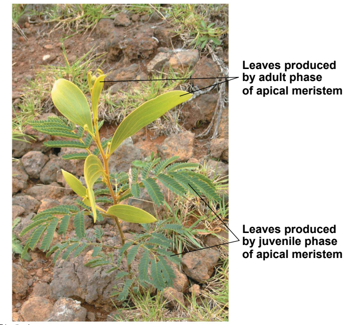
Figure 35.32



Shifts in Development: Phase Changes

- Plants pass through developmental phases, called **phase changes**, developing from a juvenile phase to an adult phase
- Phase changes occur within the shoot apical meristem
- The most obvious morphological changes typically occur in leaf size and shape

Figure 35.33

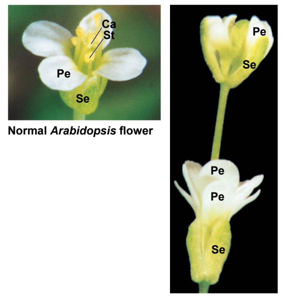


Genetic Control of Flowering

- Flower formation involves a phase change from vegetative growth to reproductive growth
- It is triggered by a combination of environmental cues and internal signals
- Transition from vegetative growth to flowering is associated with the switching on of floral **meristem identity genes**

- In a developing flower, the order of each primordium's emergence determines its fate: sepal, petal, stamen, or carpel
- Plant biologists have identified several **organ identity genes** (plant homeotic genes) that regulate the development of floral pattern
- These are *MADS-box* genes
- A mutation in a plant organ identity gene can cause abnormal floral development

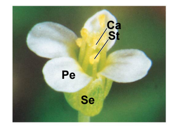
Figure 35.34



Normal *Arabidopsis* flower

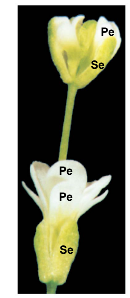
Abnormal *Arabidopsis* flower

Figure 35.34a



Normal *Arabidopsis* flower

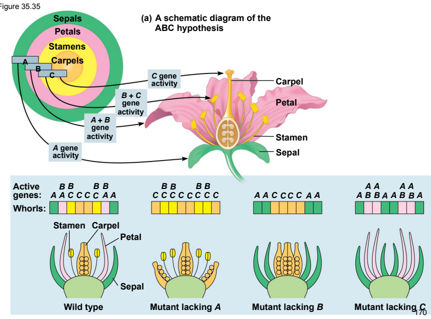
Figure 35.34b



Abnormal *Arabidopsis* flower

- Researchers have identified three classes of floral organ identity genes
- The **ABC hypothesis** of flower formation identifies how floral organ identity genes direct the formation of the four types of floral organs
- An understanding of mutants of the organ identity genes depicts how this model accounts for floral phenotypes

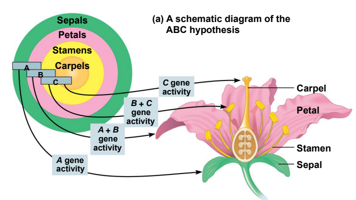
Figure 35.35



(a) A schematic diagram of the ABC hypothesis

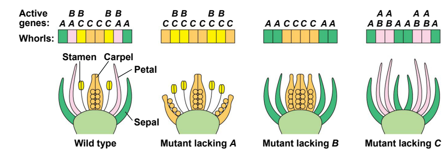
(b) Side view of flowers with organ identity mutations

Figure 35.35a



(a) A schematic diagram of the ABC hypothesis

Figure 35.35b



(b) Side view of flowers with organ identity mutations

Figure 35.UN01a

Seed Collection Site	Average Area of a Single Tooth (cm^2)		Number of Teeth per cm^2 of Leaf Area	
	Grown in Rhode Island	Grown in Florida	Grown in Rhode Island	Grown in Florida
Ontario (43.32°N)	0.017	0.017	3.9	3.2
Pennsylvania (42.12°N)	0.020	0.014	3.0	3.5
South Carolina (33.45°N)	0.024	0.028	2.3	1.9
Florida (30.65°N)	0.027	0.047	2.1	0.9

Figure 35.UN01b

Figure 35.UN03

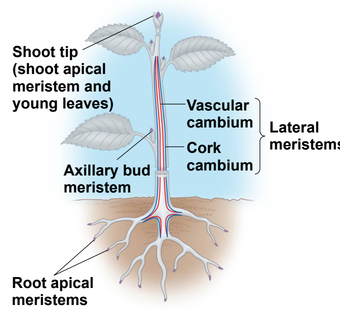


Figure 35.UN04

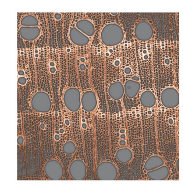


Figure 35.UN05