UNIT 6

Plant Form and Function

Chapter 35

Plant Structure, Growth, and Development

Key Concepts

35.1 The plant body has a hierarchy of organs, tissues, and cells

35.2 Meristems generate cells for new organs

35.3 Primary growth lengthens roots and shoots

35.4 Secondary growth adds girth to stems and roots in woody plants

35.5 Growth, morphogenesis, and differentiation produce the plant body

Framework

A rather large new vocabulary is needed to name the specialized cells and structures in a study of plant structure and growth. Focus your attention on how the roots, stems, and leaves of a plant are specialized to function in absorption, support, transport, protection, and photosynthesis. The plant body is composed of dermal, vascular, and ground tissue systems. Apical meristems at the tips of roots and shoots create primary growth. The lateral meristems, vascular cambium and cork cambium, create secondary growth that adds girth to stems and roots. New techniques and model systems such as *Arabidopsis* are allowing researchers to explore the molecular bases for plant growth, morphogenesis, and cellular differentiation.

Chapter Review

Plant development and structure are controlled by both genetic and environmental factors. Due to their developmental **plasticity,** no two plants are alike. Evolutionary adaptation to terrestrial environments has shaped distinctive plant **morphologies.**

35.1 The plant body has a hierarchy of organs, tissues, and cells

A plant **organ** performs a specific function and is composed of several types of **tissues,** groups of cells with a particular function.

The Three Basic Plant Organs: Roots, Stems, and Leaves As an evolutionary adaptation to the dispersed resources in a terrestrial environment, vascular plants have an underground **root system** for obtaining water and minerals from the soil and an aerial **shoot system** of stems and leaves for absorbing light and carbon dioxide for photosynthesis. The shoot system includes vegetative shoots and reproductive shoots, which, in angiosperms, are flowers.

The functions of **roots** include anchorage, absorption, and storage of food. A **taproot system** is found commonly in eudicots and gymnosperms. The one main deep root gives rise to **lateral roots** and often stores nutrients. Monocots and seedless vascular plants generally have a more shallow **fibrous root system** in which many small roots grow from the stem. Such roots are called **adventitious,** as they grow in an unusual location.

Most absorption of water and minerals occurs through tiny **root hairs,** extensions of epidermal cells that are clustered near root tips. Symbiotic associations between roots and fungi and bacteria may contribute to water and mineral absorption. Modified roots may serve various functions, including support, storage, and oxygen absorption.

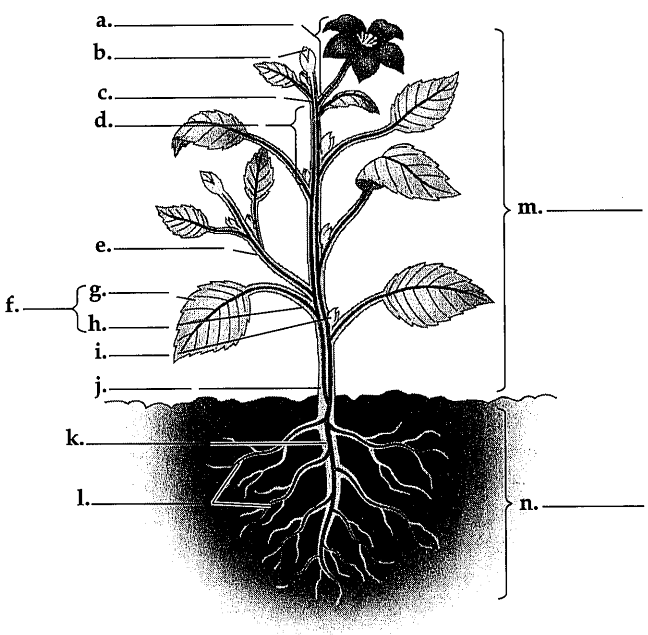
A **stem** consists of alternating **nodes,** the points at which leaves are attached, and segments between nodes, called **internodes.** An **axillary bud** is found in the angle (axil) between a leaf and the stem. A **terminal bud,** consisting of developing leaves and compacted nodes and internodes, is found at the tip or apex of a shoot. The terminal bud may exhibit **apical dominance,** inhibiting the growth of axillary buds and producing a taller plant. Axillary buds may develop into lateral shoots, or branches, with their own terminal buds, leaves, and axillary buds.

Modifications of shoots include stolons, rhizomes, tubers, and bulbs. These structures may function in asexual reproduction and food storage.

Leaves, the main photosynthetic organs of most plants, usually consist of a flattened **blade** and a **petiole,** or stalk. Many monocots lack petioles. Monocot leaves usually have parallel major **veins** (vascular tissue of leaves), whereas eudicot leaves have networks of branched veins. Leaves may be simple or compound. Modified leaves may function in support, storage, and reproduction.

■ INTERACTIVE QUESTION 35.1

Label the parts in this diagram of a flowering plant.



The Three Tissue Systems: Dermal, Vascular, and Ground **Tissue systems** are functional units of tissues that are continuous throughout the plant but have specific characteristics in each plant organ (root, stem, and leaf).

The **dermal tissue system** forms a protective outer layer. The **epidermis** is a single layer of cells that covers nonwoody plants. Older stems and roots of woody plants are covered by a protective **periderm.** Root hairs are extensions of epidermal cells near root tips. The epidermis of leaves and most stems is covered with a **cuticle,** a waxy coating that prevents excess water loss.

The **vascular tissue system** consists of **xylem** and **phloem** and functions in long-distance transport. In angiosperms, the **stele,** or vascular tissue of a root or stem, is arranged as a solid central **vascular cylinder** in roots, but as **vascular bundles** in stems and leaves.

The **ground tissue system** contains cells that function in photosynthesis, support, and storage. Ground tissue internal to vascular tissue is called **pith;** outside the vascular tissue it is called **cortex.**

Common Types of Plant Cells Cellular differentiation of plant cells may produce modifications of the cell wall and/or of the **protoplast,** the cell contents excluding the cell wall, that specialize cells for different functions.

Parenchyma cells carry on most of a plant's metabolic functions, such as photosynthesis and food storage. They usually lack secondary walls and have large central vacuoles. Most retain the ability to divide and differentiate into other types of plant cells.

Collenchyma cells lack secondary walls but have thickened primary walls. Strands or cylinders of these cells function in flexible support for young parts of the plant and elongate along with the plant.

Sclerenchyma cells have thick secondary walls strengthened with lignin. These specialized supporting cells often lose their protoplasts at maturity. **Fibers** are long, tapered cells that usually occur in threads. **Sclereids** are shorter and irregular in shape, with very thick, lignified cell walls.

The water-conducting cells of xylem die at functional maturity, leaving behind their secondary walls, which are interrupted only by scattered pits. **Tracheids,** found in all vascular plants, are long, thin, tapered cells with lignin-strengthened walls. Water passes through pits from cell to cell. **Vessel elements,** found only in angiosperms, are wider, shorter, and thinner walled, with perforations in their end walls. They align to form long tubes known as **vessels.**

In the phloem of angiosperms, sugars flow through chains of cells called **sieve-tube members,** which remain alive at functional maturity but lack nuclei, ribosomes, and vacuoles. Fluid flows through pores in the **sieve plates** in the end walls between cells. The nucleus and ribosomes of an adjacent **companion cell,** which is connected to a sieve-tube member by numerous plasmodesmata, may serve both cells.

■ INTERACTIVE QUESTION 35.2

a. Which types of plant cells are dead at functional maturity?

b. Which types of plant cells lack nuclei at functional maturity?

35.2 Meristems generate cells for new organs

Most plants exhibit **indeterminate growth,** continuing to grow as long as they live. Plant organs such as leaves and flowers, as well as animals, have **determinate growth** and stop growing after reaching a certain size. Plants may be **annuals,** which complete their life cycle in a year or less; **biennials,** which have a life cycle spanning two years; or **perennials,** which live many years.

Plants have tissues called **meristems,** which remain embryonic and perpetually divide to form new cells. **Apical meristems,** located at the tips of roots and in the buds of shoots, produce **primary growth,** resulting in the elongation of roots and shoots. **Herbaceous** (nonwoody) plants have primary growth. **Secondary growth** is an increase in diameter as new cells are produced by **lateral meristems. Vascular cambium** produces secondary xylem and phloem; **cork cambium** produces the periderm. Cells that remain to divide in a meristem are called **initials,** whereas cells that are displaced from the meristem and become specialized in developing tissues are call **derivatives.**

■ INTERACTIVE QUESTION 35.3

What types of growth occur in woody plants?

35.3 Primary growth lengthens roots and shoots

The **primary plant body,** produced by primary growth, is the entire herbaceous plant (usually) and the youngest parts of a woody plant.

Primary Growth of Roots The apical meristem of the root tip is protected by a **root cap,** which secretes a polysaccharide slime to lubricate the growth route. The **zone of cell division** includes the apical meristem and its derivatives. In the **zone of elongation,** cells lengthen to many times their original size, which pushes the root tip through the soil. Cells specialize in structure and function as the zone of elongation grades into the **zone of maturation.**

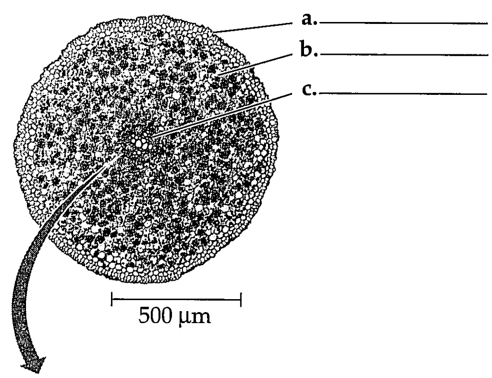
The primary tissues of a root are the epidermis, ground tissue, and vascular tissue. In most roots, xylem cells radiate from the center in spokes, with phloem in between. The vascular tissue of a monocot may have pith, a central core of undifferentiated parenchyma cells, inside rings of xylem and phloem.

The ground tissue consists of parenchyma cells in the cortex. The innermost layer of cortex is the one-cell-thick **endodermis,** which regulates the passage of materials into the vascular cylinder.

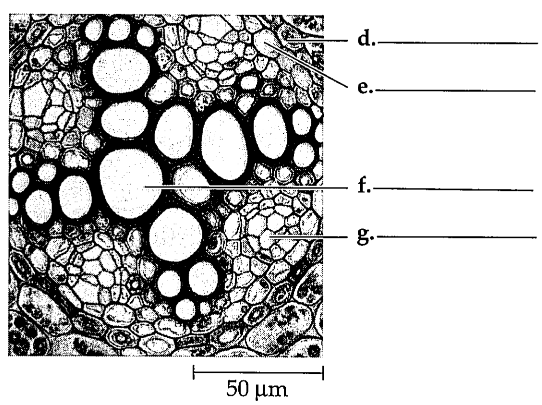
Lateral roots may develop from the **pericycle,** the outer layer of cells in the vascular cylinder. A lateral root pushes through the cortex and retains its connection with the vascular cylinder.

■ INTERACTIVE QUESTION 35.4

Label the tissues in the cross sections of a eudicot root and its vascular cylinder. Identify the functions of these tissues.



(a) Transverse section of a typical root. In the roots of typical gymnosperms and eudicots, as well as some monocots, the stele is a vascular cylinder consisting of a lobed core of xylem with phloem between the lobes.



Primary Growth of Shoots The dome-shaped mass at the tip of the terminal bud is the shoot apical meristem. **Leaf primordia** form on the sides of the apical meristem, and axillary buds develop from clumps of meristematic cells left at the bases of the leaf primordia.

Elongation of the shoot occurs by cell division and cell elongation within young internodes. In grasses and some other plants, internodes have intercalary meristems that enable shoots to continue elongation.

The epidermis of the dermal tissue system covers stems. In gymnosperms and most eudicots, vascular bundles may be arranged in a ring, with the ground tissues pith inside and cortex outside the ring. Xylem is located internal to the phloem in the vascular bundles. In most monocot stems, the vascular bundles are scattered throughout the ground tissue. A layer of collenchyma just beneath the epidermis and fiber cells of sclerenchyma within vascular bundles may strengthen the stem.

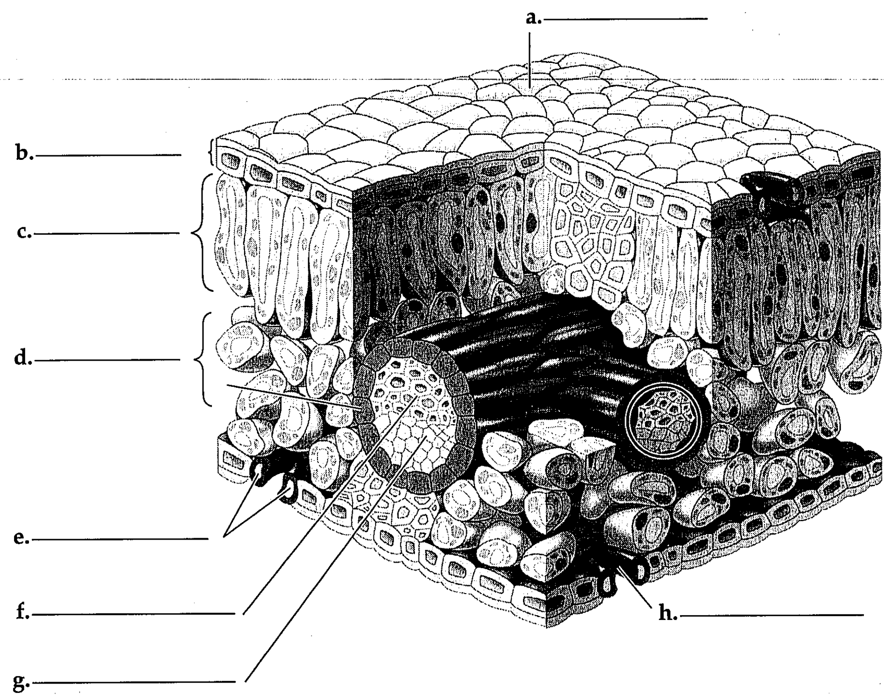
The leaf is covered by the wax-coated, tightly interlocking cells of the epidermis. **Stomata,** tiny pores flanked by **guard cells,** permit both gas exchange and transpiration, the evaporation of water from the leaf.

Mesophyll consists of parenchyma ground tissue cells containing chloroplasts. In many eudicot leaves, columnar **palisade parenchyma** is located above **spongy parenchyma,** which has loosely packed cells surrounding many air spaces.

A **leaf trace,** which is a branch of a vascular bundle in the stem, continues into the petiole and divides repeatedly within the blade of the leaf, providing support and vascular tissue to the photosynthetic mesophyll. Each vein is enclosed in a ring of prote cells called a **bundle sheath.**

■ INTERACTIVE QUESTION 35.5

Name the indicated structures in this diagram of a leaf.



35.4 Secondary growth adds girth to stems and roots in woody plants

The vascular cambium and cork cambium produce the **secondary plant body.** Secondary growth occurs in all gymnosperms and many eudicots but is rare in monocots.

■ INTERACTIVE QUESTION 35.6

Explain how primary and secondary growth can occur simultaneously in a woody stem.

The Vascular Cambium and Secondary Vascular Tissue Vascular cambium forms a continuous cylinder from a band of parenchyma cells that become meristematic, located between the primary xylem and phloem of each vascular bundle, and in the ground tissue between bundles. **Fusiform initials** produce secondary xylem to the inside and secondary phloem to the outside. **Ray initials** produce radial lines of parenchyma cells called xylem rays and phloem rays, which function in storage and lateral transport of water and nutrients.

Wood is the accumulation of secondary xylem cells with thick, lignified walls. Annual growth rings result from the seasonal cycle of cambium dormancy, early wood production (usually in the spring), and late wood production (in the summer) in temperate regions. In older trees, a central column of **heartwood** consists of older xylem with resin-filled cell cavities; the **sapwood** consists of secondary xylem that still functions in transport.

Older secondary phloem is sloughed off as bark; only that closest to the vascular cambium functions in sugar transport.

Cork Cambia and the Production of Periderm The epidermis splits off during secondary growth and is replaced by new protective tissues produced by the cork cambium, a meristematic cylinder that first forms in the outer cortex in stems and the outer pericycle in roots. The cork cambium produces a thin layered phelloderm to the inside and cork cells to the exterior, which develop suberin-impregnated walls. The protective coat formed by a cork cambium and its tissues is a layer of periderm. As secondary growth continually splits the outer layers of periderm, new cork cambia develop, eventually forming from parenchyma cells in the secondary phloem. **Lenticels** are spaces between cork cells through which gas exchange occurs. **Bark** refers to phloem and periderm.

■ INTERACTIVE QUESTION 35.7

Starting from the outside, place the letters of the tissues in the order in which they are located in a woody tree trunk.

A. primary phloem

B. secondary phloem

C. primary xylem

D. secondary xylem

E. pith

F. cork cambium

G. vascular cambium

H. cork cells

____ ____ ____ ____ ____ ____ ____ ____

35.5 Growth, morphogenesis, and differentiation produce the plant body

Growth, or the increase in mass, results from cell division and expansion. The organization of cells to create body form is called **morphogenesis.** The third developmental process, differentiation, creates cells with specific structural and functional features.

Molecular Biology: Revolutionizing the Study of Plants Modern plant biology is using new methods and new research organisms, such as *Arabidopsis thaliana*, to study the genetic control of plant development. The entire genome of *Arabidopsis* has been sequenced, and researchers are working to determine the functions of all of its 26,000 (of 15,000 different types) genes by 2010. A major goal of **systems biology** is to track which genes are activated and where during a plants' development.

Growth: Cell Division and Cell Expansion The plane and symmetry of plant cell division is important in determining form. In **asymmetrical cell division,** one daughter cell receives more cytoplasm than the other, often leading to a key developmental event.

The plane of cell division is determined by the **preprophase band,** a ring of cytoskeletal microtubules that forms during late interphase. The microtubules disperse but leave behind an ordered array of actin microfilaments that indicate the plane of cell division.

About 90% of plant cell growth is due to the uptake of water into the central vacuole. This economical means of cell elongation produces the rapid growth of shoots and roots. When enzymes break the cross-links in the cell wall, the restraint on the turgid cell is reduced and water enters the cell by osmosis. Cells expand in a direction perpendicular to the orientation of the cellulose microfibrils in the inner layers of the cell wall. This orientation of microfibrils was determined by the orientation of microtubules in the outer cytoplasm.

In the squat-bodied *fass* mutants of *Arabidopsis*, preprophase bands are not formed in mitosis and the random distribution of cortical microtubules leads to the random arrangement of cellulose microfibrils. The defects in microtubule organization result in cells that divide in a random arrangement and expand equally in all directions.

■ INTERACTIVE QUESTION 35.8

Review the role of microtubules in the orientation of plant cell division and expansion.

Morphogenesis and Pattern Formation **Pattern formation** is the characteristic development of structures in specific locations. Pattern formation appears to depend on **positional information,** signals that indicate a cell's location within a developing organ and thus direct its growth and differentiation. An embryonic cell may detect its location by gradients of molecules, probably proteins or mRNAs, that diffuse from specific locations in a developing structure.

Plants typically have an axial **polarity** with a root end and a shoot end. The asymmetric first division of the zygote establishes the shoot–root polarity.

Plants have homeotic genes that regulate key developmental events. In many plants, the *KNOTTED-1* homeotic gene influences leaf morphology. Its overexpression in tomato plants results in "super-compound" leaves.

Gene Expression and Control of Cellular Differentiation Differential gene expression within genetically identical cells leads to their differentiation into the diverse cell types in a plant. In the root epidermis of *Arabidopsis,* the homeotic gene *GLABRA-2* is expressed in epidermal cells that are in contact with only one underlying cortical cell, and these cells do not develop root hairs. The gene is not expressed in those cells in contact with two cortical cells, and they differentiate into root hair cells. A mutant gene results in every root epidermal cell developing a root hair.

Location and a Cell's Developmental Fate Using clonal analysis, researchers are able to identify cells in the apical meristem and follow their lineages to pinpoint when the developmental fate of a cell becomes determined. Apparently the cells of the meristem are not committed to the formation of specific organs and tissues. A cell's final position in a developing organ determines what type of cell it will become.

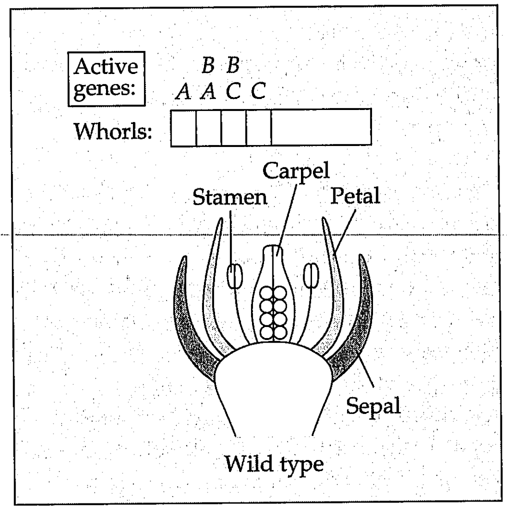
Shifts in Development: Phase Changes In a process known as a **phase change,** the apical meristem can switch from one developmental phase to another, such as from producing juvenile vegetative nodes and internodes to laying down mature nodes. A node's developmental phase is fixed when it is produced, and thus both juvenile and mature leaves can coexist along the shoots of a plant.

Genetic Control of Flowering In the transition from a vegetative shoot to a reproductive shoot (flower), **meristem identity genes** are expressed that code for transcription factors that activate the genes necessary for floral meristem development.

The four floral organs develop from leaf primordial in four concentric whorls: sepals, petals, stamens, and carpels. Some of the **organ identity genes** that determine this characteristic floral pattern have been identified, and their expression seems to be influenced by positional information. Mutations of organ-identity genes result in the placement of one type of floral organ where another type would normally develop. The **ABC model** of flower formation proposes three classes of organ identity genes, each of which affects two adjacent whorls. This model explains the phenotypes of mutants lacking *A, B,* or *C* gene expression, with the additional observation that activity of the *A* or *C* gene inhibits the expression of the other. If either *A* or *C* is nonfunctional, the other gene is expressed in its place.

■ INTERACTIVE QUESTION 35.9

This diagram of the ABC model shows the active genes in each whorl and the resulting anatomy of a wild-type flower.



a. Fill in the table below to show which organs are produced in the whorls in a normal flower. In a mutant that lacks a functional gene *A,* what gene expression pattern and resulting flower organ arrangement would be produced? (Remember that a lack of *A* activity removes the inhibition of gene *C.*)

Whorl	Genes Active	Organs in Normal	Genes Active in Mutant *A*	Organs in Mutant *A*
1	*A*			
2	*AB*			
3	*BC*			
4	*C*			

b. If you had a double-mutant plant that had no gene activity for *B* or *C,* what would the resulting flower look like?

Word Roots

apic- = the tip; **meristo-** = divided (*apical meristems:* embryonic plant tissue on the tips of roots and in the buds of shoots that supplies cells for the plant to grow)

a- = not, without; **-symmetr** = symmetrical (*asymmetric cell division:* cell division in which one daughter cell receives more cytoplasm than the other during mitosis)

bienn- = every 2 years (*biennial:* a plant that requires two years to complete its life cycle)

coll- = glue; **-enchyma** = an infusion (*collenchyma cell:* a flexible plant cell type that occurs in strands or cylinders that support young parts of the plant without restraining growth)

endo- = inner; **derm-** = skin (*endodermis:* the innermost layer of the cortex in plants roots)

epi- = over (*epidermis:* the dermal tissue system in plants; the outer covering of animals)

fusi- = a spindle (*fusiform initials:* the cambium cells within the vascular bundles; the name refers to the tapered ends of these elongated cells)

inter- = between (*internode:* the segment of a plant stem between the points where leaves are attached)

meso- = middle; **-phyll** = a leaf (*mesophyll:* the ground tissue of a leaf, sandwiched between the upper and lower epidermis and specialized for photosynthesis)

morpho- = form; **-genesis** = origin (*morphogenesis:* the development of body shape and organization during ontogeny)

perenni- = through the year (*perennial:* a plant that lives for many years)

peri- = around; **-cycle** = a circle (*pericycle:* a layer of cells just inside the endodermis of a root that may become meristematic and begin dividing again)

phloe- = the bark of a tree (*phloem:* the portion of the vascular system in plants consisting of living cells arranged into elongated tubes that transport sugar and other organic nutrients throughout the plant)

pro- = before (*procambium:* a primary meristem of roots and shoots that forms the vascular tissue)

proto- = first; **-plast** = formed, molded (*protoplast:* the contents of a plant cell exclusive of the cell wall)

sclero- = hard (*sclereid:* a short, irregular sclerenchyma cell in nutshells and seed coats and scattered through the parenchyma of some plants)

trachei- = the windpipe (*tracheids:* a water-conducting and supportive element of xylem composed of long, thin cells with tapered ends and walls hardened with lignin)

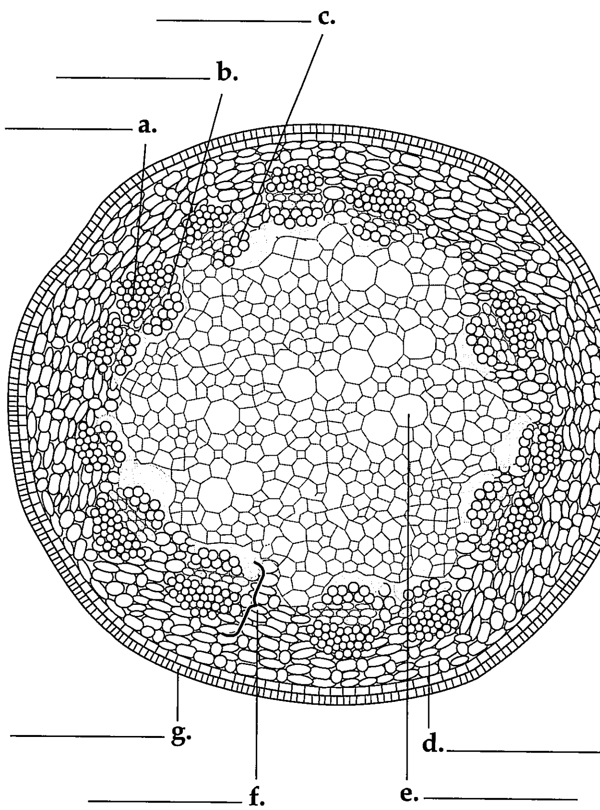
trans- = across (*transpiration:* the evaporative loss of water from a plant)

vascula- = a little vessel (*vascular tissue:* plant tissue consisting of cells joined into tubes that transport water and nutrients throughout the plant body)

xyl- = wood (*xylem:* the tube-shaped, nonliving portion of the vascular system in plants that carries water and minerals from the roots to the rest of the plant)

Structure Your Knowledge

1. How does the indeterminate growth pattern of plants lead to developmental plasticity? What is the adaptive advantage of such plasticity?
2. In this cross section of a young stem, label the indicated structures. Is this a stem of a monocot or a eudicot? How can you tell?



Test Your Knowledge

MATCHING: *Match the plant tissue with its description.*

____	1. sclerenchyma	A.	layer from which lateral roots originate
____	2. collenchyma	B.	tapered xylem cells with lignin in cell walls
____	3. tracheids	C.	parenchyma cells with chloroplasts in leaves
____	4. fibers	D.	protective coat made of cork and cork cambium

____ 5. fusiform initials	E. bundles of long sclerenchyma cells
____ 6. pericycle	F. supporting cells with thickened primary walls
____ 7. mesophyll	G. parenchyma cells inside vascular ring in eudicot stem
____ 8. periderm	H. supporting cells with thick secondary walls
____ 9. endodermis	I. cambium cells that produce secondary xylem and phloem
____ 10. pith	J. cell layer in root regulating movement into vascular cylinder

MULTIPLE CHOICE: *Choose the one best answer.*

1. Which of the following is *incorrect?* Monocots typically have
   a. a taproot rather than a fibrous root system.
   b. leaves with parallel veins rather than branching venation.
   c. no secondary growth.
   d. scattered vascular bundles in the stem rather than bundles in a ring.
   e. pith in the center of the vascular cylinder in the root.
2. Which of the following is *incorrectly* paired with its function?
   a. ray initials—form radial xylem and phloem rays
   b. lenticels—gas exchange in woody stem
   c. root hairs—absorption of water and dissolved minerals
   d. root cap—protects root as it pushes through soil
   e. procambium—meristematic tissue that forms protective layer of cork
3. Axillary buds
   a. may exhibit apical dominance over the terminal bud.
   b. form at nodes in the angle where leaves join the stem.
   c. grow out from the pericycle layer.
   d. are formed from intercalary meristems.
   e. only develop into vegetative shoots.
4. A leaf trace is
   a. a petiole.
   b. the outline of the vascular bundles in a leaf.
   c. vascular bundle that extends into a leaf.
   d. a tiny bulge on the flank of the apical dome that grows into a leaf.
   e. a system of plant identification based on leaf morphology.
5. Which of the following structures of a plant shows determinate growth?
   a. roots
   b. vegetative shoots
   c. adventitious roots
   d. leaves
   e. No parts of a plant show determinate growth.
6. Morphogenesis in plants results from
   a. differences in the plane of cell division and the direction of cell expansion.
   b. migration of cells from the apical meristems to the dermal, vascular, and ground tissue systems.
   c. the differentiation of cells within the apical meristem.
   d. cells moving from the zone of elongation to the zone of maturation.
   e. the expression of meristem identity genes.
7. Which of the following is *incorrectly* paired with the length of its life cycle?
   a. pine tree—perennial
   b. rose bush—perennial
   c. carrot—biennial
   d. marigold—annual
   e. corn—biennial
8. Secondary xylem and phloem are produced in a root by the
   a. pericycle.
   b. endodermis.
   c. vascular cambium.
   d. apical meristem.
   e. cork cambium.
9. Bark consists of
   a. secondary phloem.
   b. periderm.
   c. cork cells.
   d. cork cambium.
   e. all of the above.

10. Sieve-tube members
    a. are responsible for lateral transport through a woody stem.
    b. control the activities of phloem cells that have no nuclei or ribosomes.
    c. have spiral thickenings that allow the cell to elongate along with a young shoot.
    d. are transport cells with sieve plates in the end walls between cells.
    e. are tapered water transport cells with pits.

11. Which of the following cells are dead at functional maturity?
    a. tracheids
    b. cork cells
    c. vessel elements
    d. sclerenchyma cells
    e. all of the above

12. Clonal analysis of cells of the shoot apex indicates that
    a. organ-identity gene mutations substitute one body part for another.
    b. a cell's developmental fate is more influenced by position effects than by its meristematic lineage.
    c. cellular differentiation results from regulation of gene expression resulting in production of different proteins in different cells.
    d. all cells were derived from the same parent cell.
    e. the lateral meristem produces the dermal, vascular, and ground tissue systems.

13. In what direction does a plant cell enlarge?
    a. toward the basal end as a result of positional information
    b. parallel to the orientation of the preprophase band of microtubules
    c. perpendicular to the orientation of cellulose microfibrils in the cell wall
    d. in the direction from which water flows into the cell
    e. perpendicular to the internodes

14. What do organ identity genes code for?
    a. the three tissue systems
    b. pollen and egg cells
    c. transcription factors that control development of floral organs
    d. signals that change a vegetative shoot into a floral meristem
    e. the root and shoot meristems

15. What is a usual sign of the change of the apical meristem from the juvenile to the mature phase?
    a. the production of a flower
    b. the initiation of secondary growth
    c. the production of longer internodes
    d. the activation of axillary buds
    e. a change in the morphology of leaves produced at nodes

16. Which of the following is essential to establishing the axial polarity of a plant?
    a. expression of different homeotic genes in the shoot and root meristems
    b. orientation of cortical microtubules perpendicular to the ground
    c. the expression of the *GLABRA-2* gene in the shoot but not the root
    d. the asymmetric first division of the zygote
    e. the proper orientation of microtubules that then orient cellulose-microfibrils