Chapter 5

The Shoot System I: The Stem

KEY CONCEPTS

1. The shoot system is composed of the stem and its lateral appendages: leaves, buds, and flowers. Leaves are arranged in different patterns (phyllotaxis): alternate, opposite, whorled, and spiral.

2. Stems provide support to the leaves, buds, and flowers. They conduct water and nutrients and produce new cells in meristems (shoot apical meristem, primary and secondary meristems).

3. Dicot stems and monocot stems are usually different. Dicot stems tend to have vascular bundles distributed in a ring, whereas in monocot stems they tend to be scattered.

4. Stems are composed of the following: epidermis, cortex and pith, xylem and phloem, and periderm.

5. Secondary xylem is formed by the division of cells in the vascular cambium and is called wood. The bark is composed of all of the tissues outside the vascular cambium, including the periderm (formed from cork cambium) and the secondary phloem.

6. Several different types of modified stems (rhizomes, spines, and others) have important functions.

5.1 THE FUNCTIONS AND ORGANIZATION OF THE SHOOT SYSTEM

The shoot system of a typical flowering plant consists of the stem and the attached leaves, buds, flowers, and fruits. The leaves are displayed in a way that maximizes their exposure to sunlight. Flowers and fruits are located on stems in positions that allow for pollination and the dispersal of fruits and seeds. Internally, stems provide pathways for the movement of water and dissolved minerals from the roots into the leaves and for food synthesized in leaves to move into roots. Some stems are modified for different functions such as the storage of water and various food substances.

The stem is actually composed of repeated units called modules. A module is a segment of stem-- an internode--plus the leaf and bud attached to the stem (Fig. 5.1). The point of attachment is called a node.

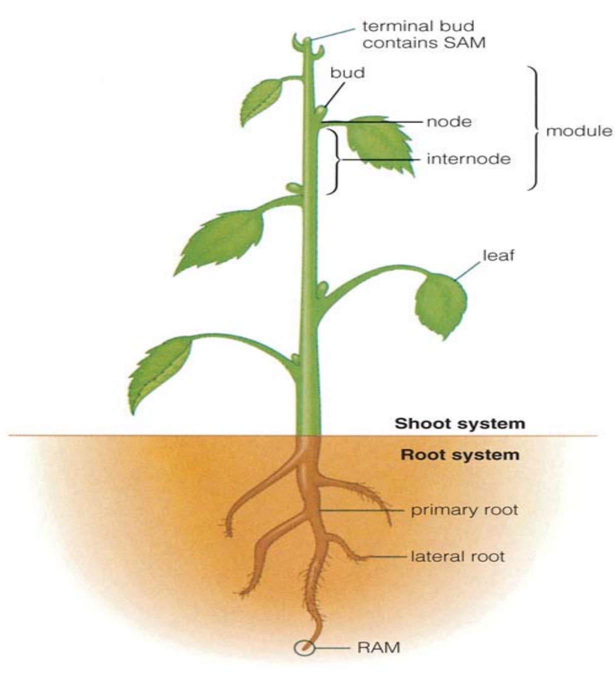


Figure 5.1. The shoot system and its parts.

The shoot apical meristems (SAM) and primary meristems of the stem are located in buds at the ends of the branches and just above the nodes. Further down the stem in some plants are secondary meristems, which make secondary tissues. These meristems produce new cells and act as sites for the start of cell elongation and differentiation.

Flowering plants are divided into two groups: dicotyledonous plants (dicots) and monocotyledonous plants (monocots). One of the bases for this division is that the dicots--such as peas (*Pisum* sp.) and oaks (*Quercus* sp.)--produce embryos with two cotyledons (seed leaves), whereas monocots--such as corn (*Zea mays*) and onions (*Allium cepa*)--produce embryos with only one (see Chapter 13). The stems of these two groups also have major differences in the distribution of their tissues (Fig. 5.2) and in the operation of their meristems. As we examine primary and secondary growth in stems, we will contrast the anatomy of dicots and monocots.

5.2 PRIMARY GROWTH AND STEM ANATOMY

Primary Tissues of Dicot Stems Develop from the Primary Meristems

The shoot apical meristem (SAM) is composed of dividing cells. It is responsible for the initiation of new leaves and buds and for making the three primary meristems (Fig. 5.3). The three primary meristems--protoderm, ground meristem, and procambium--and their tissue products are discussed in the following sections.

PROTODERM TO EPIDERMIS The outermost layer of cells in the shoot tip is the protoderm. This layer is called a primary meristem because its cells are still dividing and because primary meristems differentiate into primary tissues. When the cells of the protoderm stop dividing and mature, they are called *epidermis* (Fig. 5.4). Epidermal cells, guard cells, different kinds of trichomes or hairs, and a cuticle make up the epidermis (see Chapter 4).

GROUND MERISTEM TO PITH AND CORTEX In the very center of the shoot tip and just inside the protoderm is the *ground meristem* (Figs. 5.3, 5.4). These cells slowly lose their ability to divide, and they differentiate mostly into parenchyma cells of the cortex (the cylinder of cells just inside the epidermis) and the pith (the core of cells in the center of the stem) (Fig. 5.2b). Along with their different positions in the stem, the cortex and pith have different functions. The parenchyma cells nearest the outside of the cortex sometimes contain chloroplasts for photosynthesis. Sometimes, the parenchyma cells of the cortex or pith store starch. The pith region of the stem is some plants may become hollow by the breakdown of the centrally located parenchyma cells.

PROCAMBIUM TO PRIMARY XYLEM AND PHLOEM The *procambium* tends to form as small bundles (Figs. 5.3, 5.4) of relatively thin, long cells with dense cytoplasm. The bundles are usually arranged in a ring just inside the outer cylinder of ground meristem and below the SAM. Procambium cells divide, and then at some position down the axis they stop dividing and differentiate into primary xylem and primary phloem. Each bundle of procambium becomes a vascular bundle, with primary xylem cells toward the inside of the stem and primary phloem cells toward the outside (Fig. 5.2). In plants exhibiting secondary growth, some procambium between the primary xylem and phloem remains undifferentiated; such cells are called residual procambium (Fig. 5.4d).

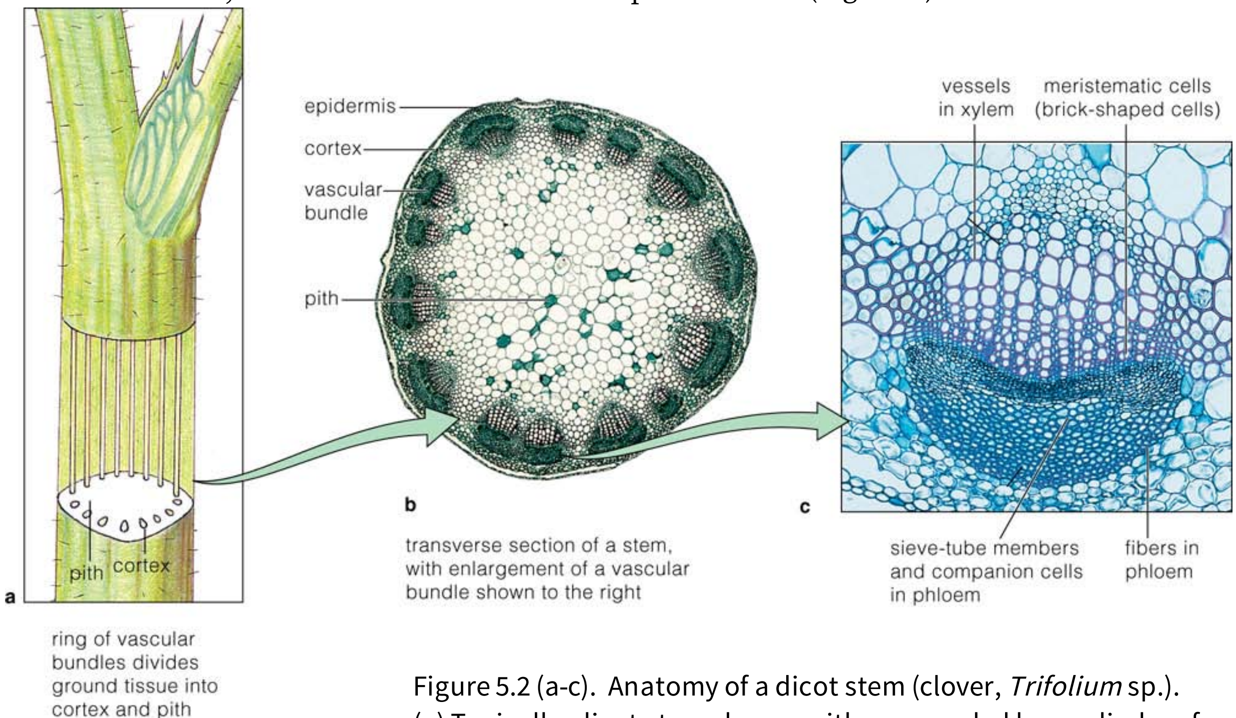


Figure 5.2 (a-c). Anatomy of a dicot stem (clover, *Trifolium* sp.). (a) Typically, dicot stems have a pith surrounded by a cylinder of vascular bundles; (b) X37; (c) These bundles usually have primary phloem toward the outside and primary xylem toward the inside. X266.

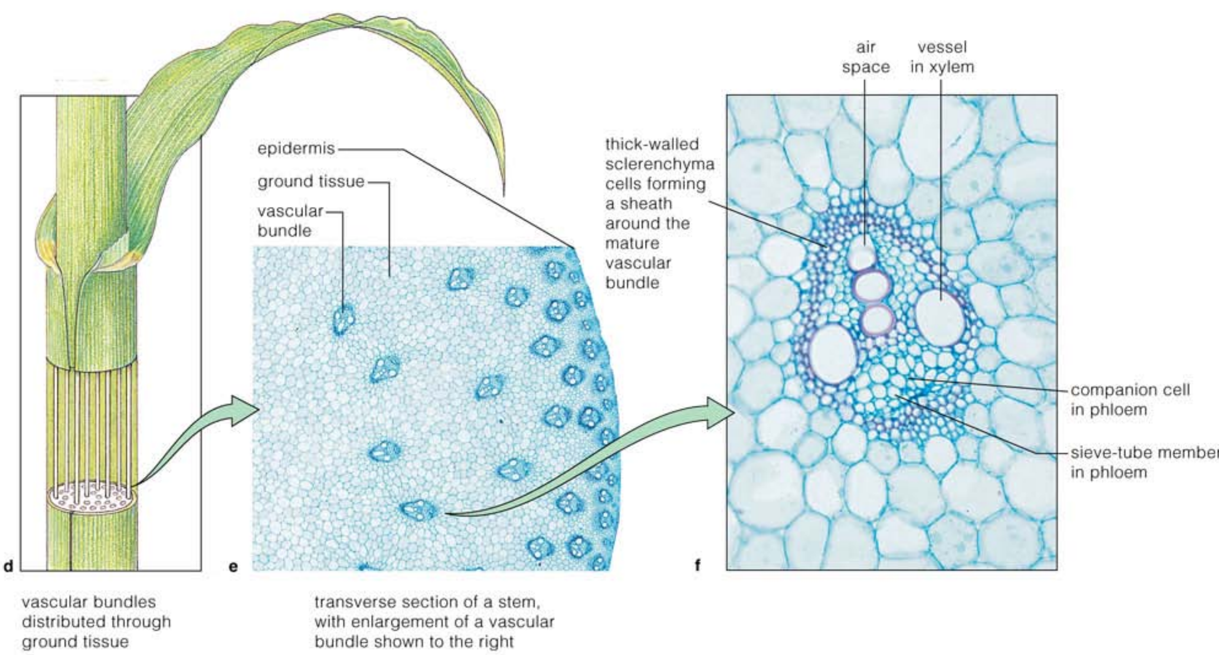


Figure 5.2 (d-f). Anatomy of a monocot stem (corn, *Zea mays*). (d) Typically, monocot stems have scattered vascular bundles; (e) X14; (f) The primary phloem is usually positioned toward the outside. X270.

The Distribution of the Primary Vascular Bundles Depends on the Position of Leaves

Vascular bundles in dicot stems are distributed in a vascular cylinder. The vascular bundles that network into the attached leaves are called leaf traces (Fig. 5.4a). The organization of primary vascular bundles in stems depends on the number and distribution of leaves and on the number of traces that branch into the leaves (Fig. 5.5) and also into buds. The number of vascular bundles in the vascular cylinder and the number of leaf traces differ by species and are dependent on the number and arrangement of leaves.

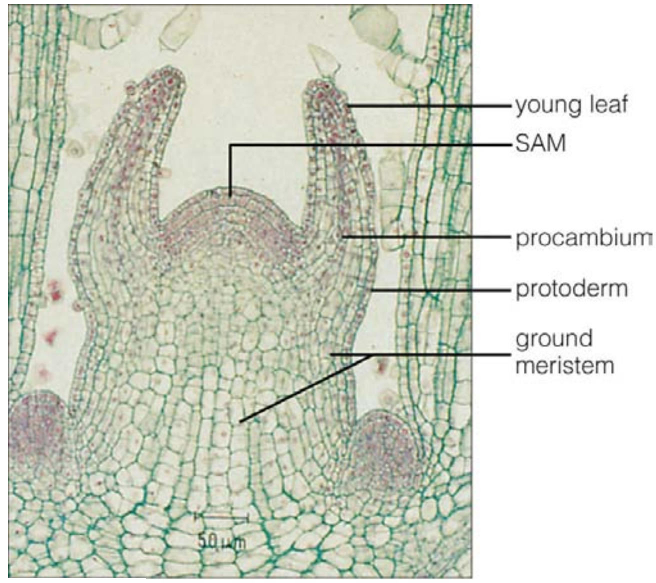


Figure 5.3. Shoot apex of *Coleus blumei*, a common houseplant. X114

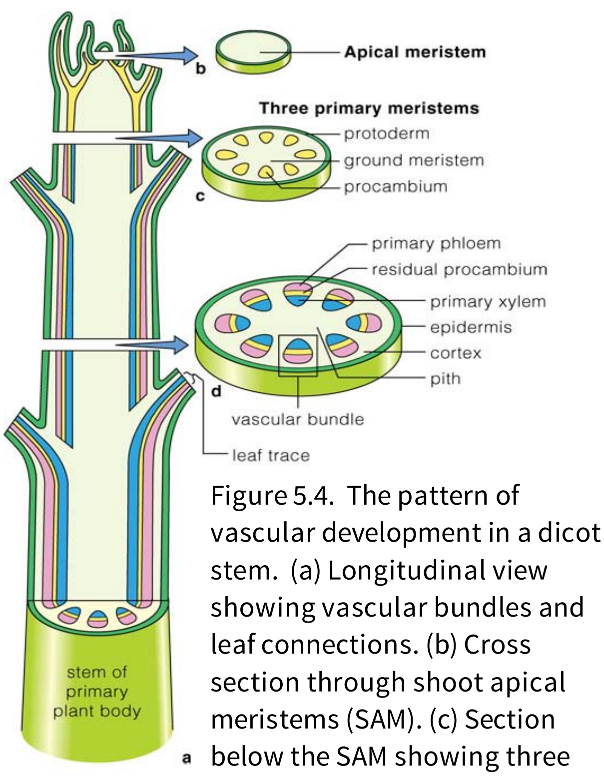


Figure 5.4. The pattern of vascular development in a dicot stem. (a) Longitudinal view showing vascular bundles and leaf connections. (b) Cross section through shoot apical meristems (SAM). (c) Section below the SAM showing three primary meristems. (d) Section showing development of procambium into primary phloem and primary xylem. Protoderms becomes epidermis; ground meristems becomes pith and cortex

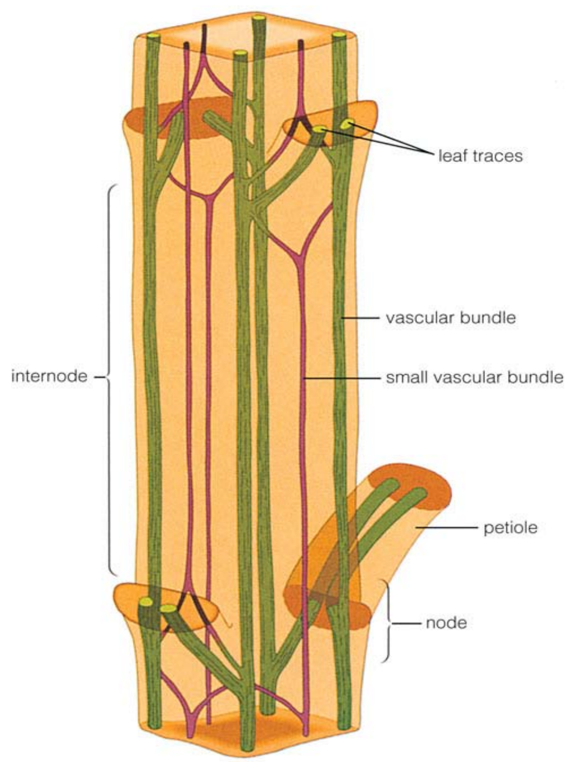


Figure 5.5. Three dimensional view of primary vascular system of a *Coleus* stem. There is a single large vascular bundle in each corner of the square stem with a smaller bundle on each side. Two traces go to each leaf.

The arrangement of leaves on the axis of the stem is called *phyllotaxis* (*phyllo-* is Greek for "leaf," and *-taxis* is Greek for "arrangement"). There are four basic patterns of phyllotaxis (Fig. 5.6). Plants with alternate phyllotaxis have only one leaf per node, and the leaves are positioned 180° from each other. The angle separating one leaf or set of leaves from another is called the *angle of divergence*. Opposite phyllotaxis means that the shoot has two leaves per node; the angle of divergence between leaves in successive sets is 90°. In whorled phyllotaxis there are three or more leaves per node, and the angle of divergence between successive sets of leaves depends on the leaf number per set. The angle is 60° in plants with three leaves per node (Fig. 5.6c). Plants with spiral phyllotaxis have one leaf per node, and the angle of divergence between leaves is 137.5° (Fig. 5.6d).

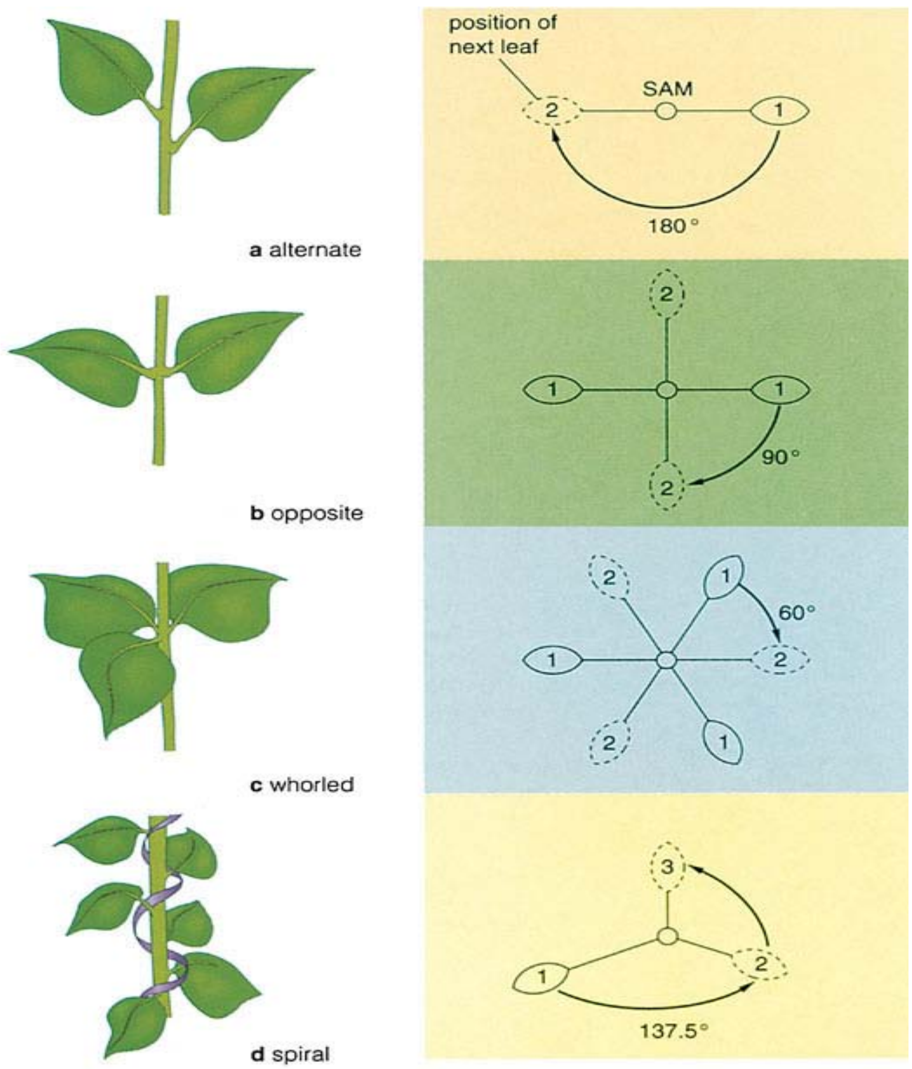


Figure 5.6. The four basic patterns of leaf arrangement (phyllotaxis): (a) "Alternate" has one leaf per node and a 180° angle of divergence between leaves. (b) "Opposite" has two leaves per node and 90° between sets of leaves; (c) "Whorled" usually has three to five leaves per node; in the case of three leaves per node the angle of divergence is 60°; (d) "Spiral" has one leaf per node and 137.5° between leaves.

Primary Growth Differs in Monocot and Dicot Stems

Monocot stems differ in several ways from the patterns described for dicot stems. One main difference is that the vascular bundles tend to be scattered throughout the stem instead of being in a ring (see Fig. 5.2). The terms *pith* and *cortex* are usually not used when the bundles are scattered; instead, the term *ground tissue* is used for all the parenchyma tissue surrounding the vascular bundles. There are some exceptions; wheat (*Triticum* sp.) stems, for example, are hollow in the stem internodes (Fig. 5.7), rather than having ground tissue there.

If you were to compare the shapes of a monocot stem and a dicot stem, one of the first things you would notice is that a monocot stem is about the same diameter near its apex as at its base. This shape is due primarily to the activity of the **primary thickening meristem** (PTM), which is absent in dicot stems. The PTM is unique in contributing to both elongation and lateral growth, a characteristic resulting from its umbrella-like shape (Fig. 5.8). The SAM and the primary meristems are also present in these tips.

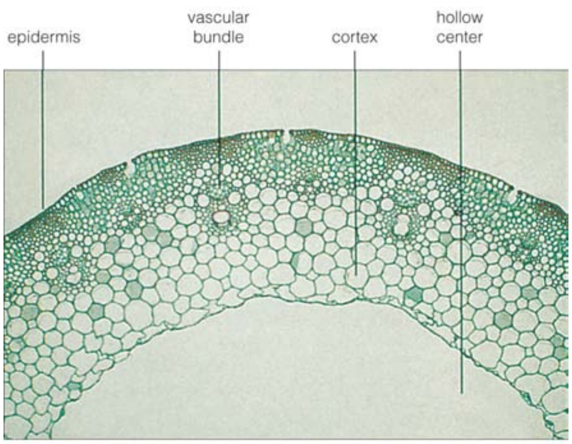


Figure 5.7 (above). Cross section of a hollow monocot wheat stem (*Triticum* sp.). X38.

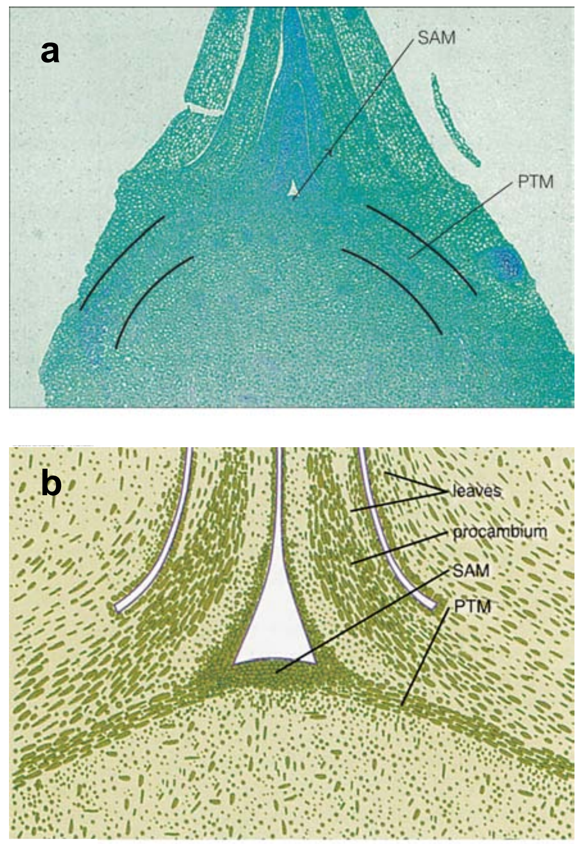


Figure 5.8 (right). (a) Longitudinal section of Iris shoot apex to show the primary thickening meristem (PTM). X108. (b) Diagram of a similar apex to more clearly show the "umbrella-shaped" PTM.

5.3 SECONDARY GROWTH AND THE ANATOMY OF WOOD

Most monocots and many dicots show little or no secondary growth. These are herbaceous (nonwoody) plants, which normally complete their life cycle in one growing season. By contrast, many other dicots, such as oaks (*Quercus* sp.) and maples (*Acer* sp.), and gymnosperms, such as pines (*Pinus* sp.) and firs (*Abies* sp.), show secondary growth starting in their first year of growth. In some plants this continues for many, even hundreds, of years; these are called woody plants.

Secondary Xylem and Phloem Develop from Vascular Cambium

Woody plants develop thicker, more massive stems because of the growth of secondary xylem and phloem from their secondary meristems. The first step in making secondary xylem and phloem is to form the vascular cambium (plural, cambia). Development of the vascular cambium involves coordinated cell division in the *residual procambium* inside the vascular bundles and the parenchyma cells between the bundles (Fig. 5.9). The signal for this cell division is probably given by a plant hormone. When the residual procambium cells divide, they are referred to as **fascicular cambium** (fasciculus is a Latin word for "bundle"). Next, the cells between the vascular bundles divide; these are referred to as the **interfascicular cambium** ("between the bundles"). The parenchyma cells near the bundles divide first, and the adjoining cells divide until a complete ring forms (Figs. 5.9, 5.10). Once the cylinder of dividing cells--the fascicular cambium plus the interfascicular cambium--is complete, it is called **vascular cambium** (Fig. 5.9).

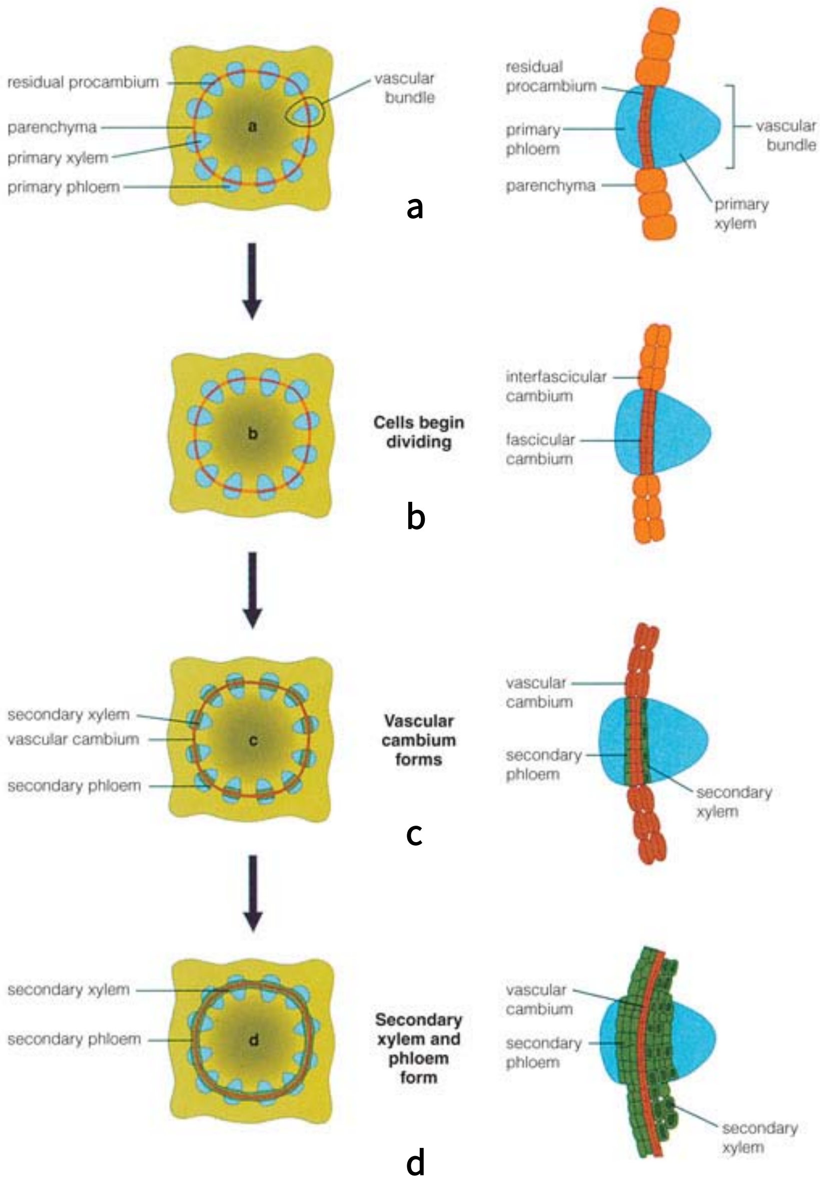


Figure 5.9. Formation of the vascular cambium. (a) At the completion of primary growth, some residual procambium cells remain between the primary xylem and primary phloem, and parenchyma cells occur between the vascular bundles. (b) After the cells begin dividing, the residual procambium is now called the fascicular cambium, and the cells between the bundles are now called the interfascicular cambium. (c) When the fascicular and interfascicular cambia are all dividing and become connected as a ring, they are called the vascular cambium. (d) Secondary xylem (inside) and secondary phloem (outside) form from the vascular cambium.

The vascular cambium is an interesting meristem in that it is only one or two cells thick but divides in two directions. The cells formed to the outside become secondary phloem, and the cells formed to the inside become secondary xylem (Figs. 5.9, 5.10). Figure 5.11 summarizes the successive divisions that contribute to thickening the secondary xylem and phloem. Vascular cambium cells produce more xylem cells than phloem cells.

Some vascular cambium cells, called **fusiform initials**, form into cells of the **axial system**; vessel members are examples (Figs. 5.12, 5.13). The cells of the **ray system** are formed from vascular cambium cells called **ray initials**. The rays are composed of only two different cell types--ray parenchyma cells and ray tracheids. The cells of the axial system function in the longitudinal movement of water and minerals; the cells of the ray system transport water and minerals radially.

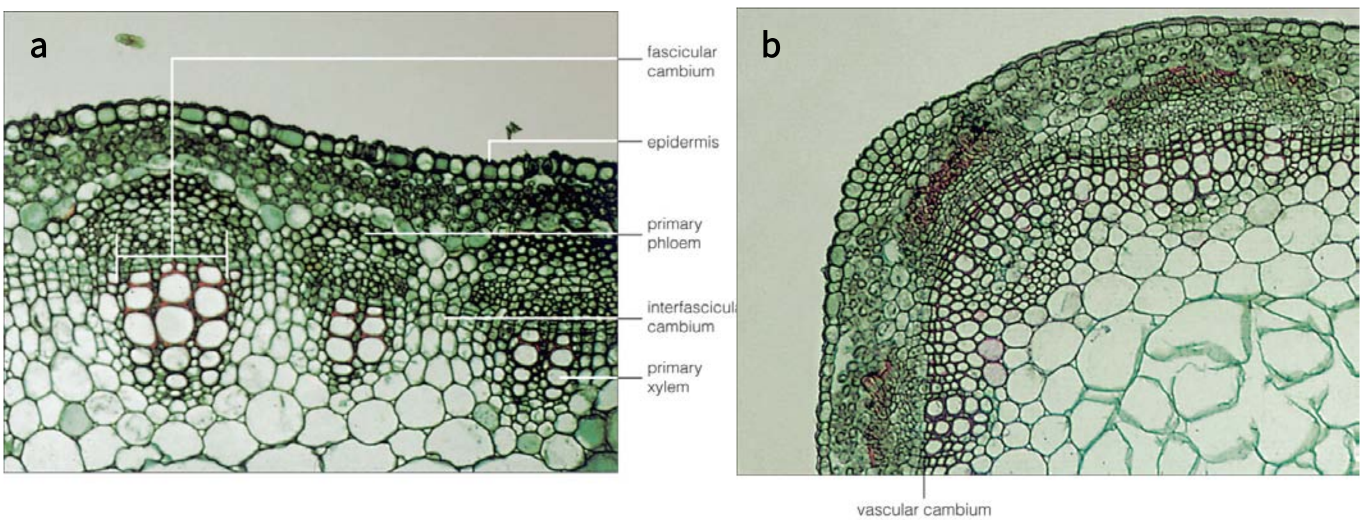


Figure 5.10. Cross sections of an alfalfa (*Medicago sativa*) stem, showing (a) the location of the fascicular and interfascicular cambia. X191 and (b) some secondary vascular tissue. X178.

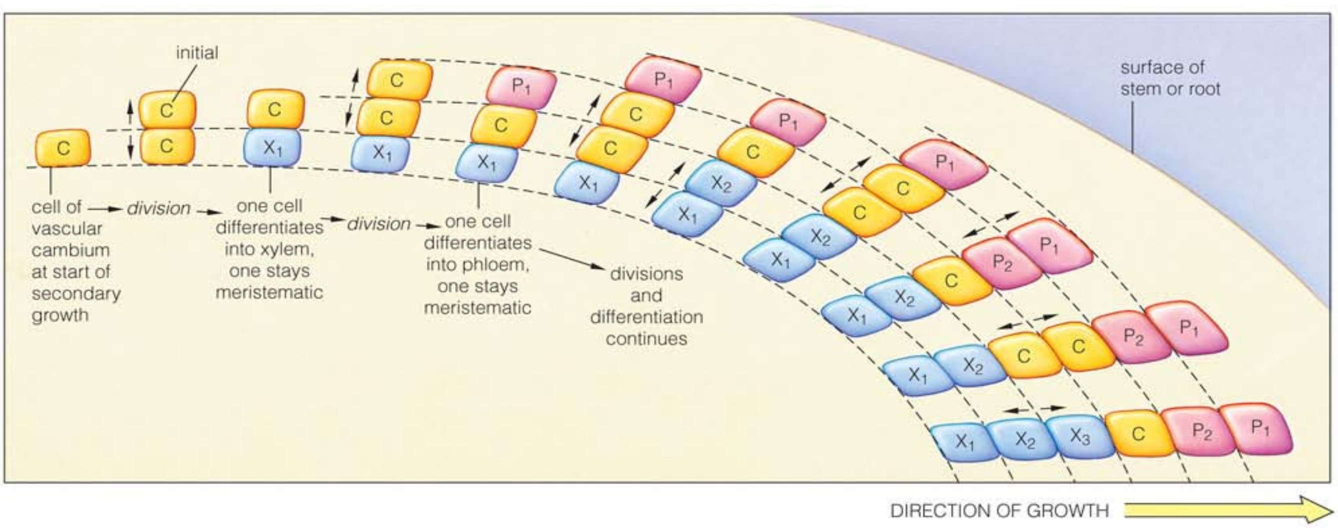


Figure 5.11. Drawing of the divisions of vascular cambium cells through a growing season. Cells labeled (C) are the initial cells; their derivative cells become secondary phloem to the outside (P1, P2…) and secondary xylem to the inside (X1, X2…). The result of this is that the stem gets wider and the vascular cambium keeps increasing in circumference and moving outward.

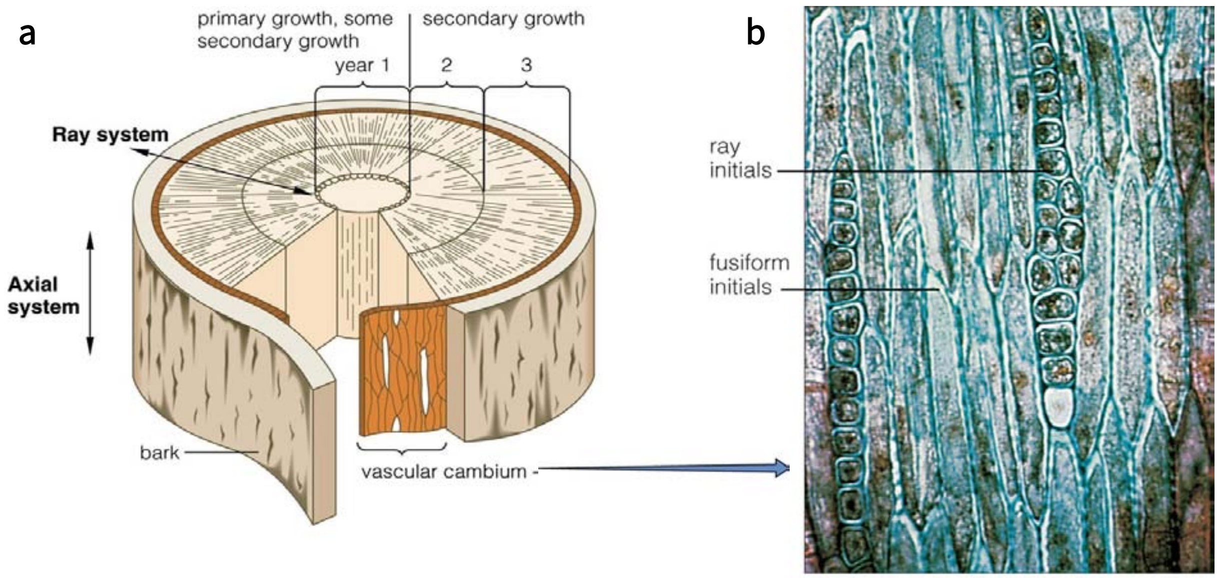
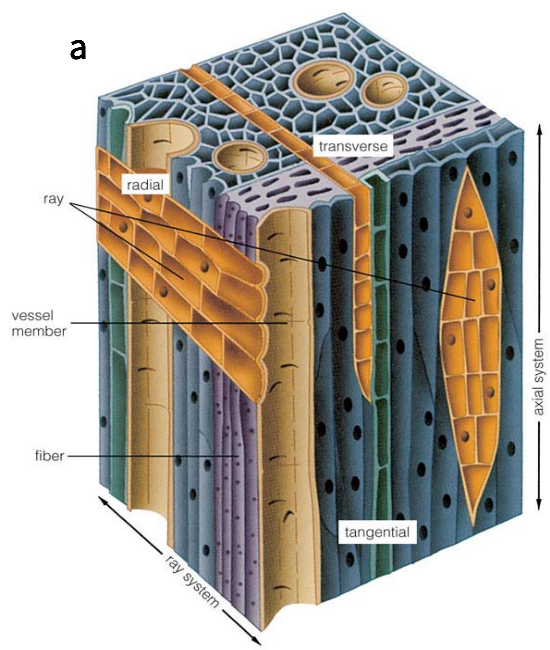


Figure 5.12. (a) Drawing of a four year old woody stem showing the growth increments as annual rings. The lines radiating from the center are the rays, all the rays together make up the ray system. All the other cells in the wood make up the axial system. Bark refers to all the tissue from the vascular cambium to the outside. (b) The vascular cambium has two types of initial cells; the ray initials make the rays, and the fusiform initials make the cells of the axial system. X275.



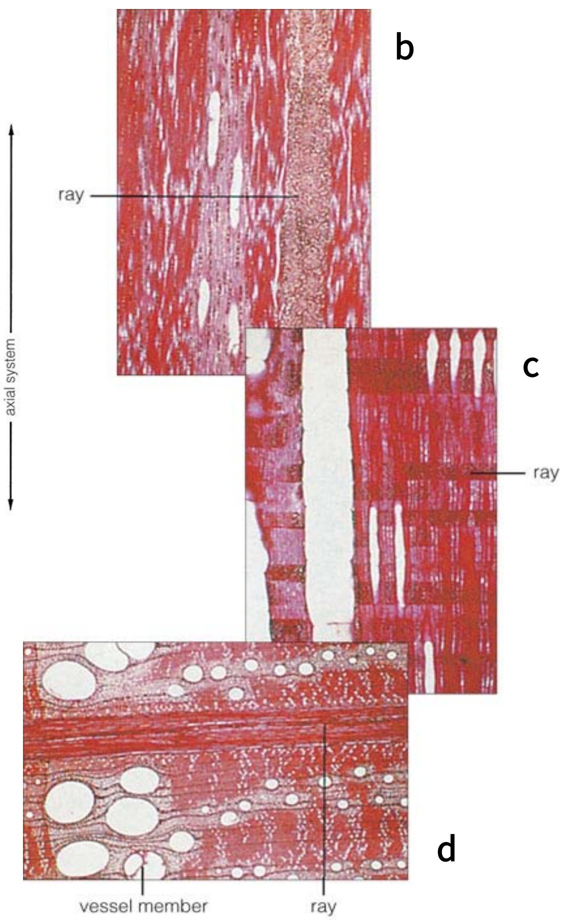


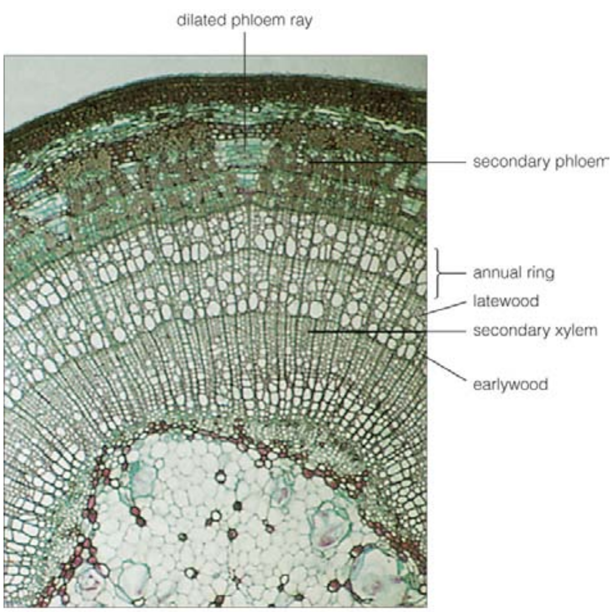
Figure 5.13. Structure of Red oak (*Quercus rubra*) wood. (a) Three-dimensional diagram showing the cells as they appear in three in three planes of view. (b) In the tangential section the ends of the large rays are visible. (c) Radial sections show the side of the rays. (d) In the transverse section the annual rings, springwood and summerwood are obvious. (b,c,d) X20.

Wood Is Composed of Secondary Xylem

The **secondary xylem** is collectively called *wood*. Examining thin sections of wood under a microscope reveals its many distinctive characteristics. Typically, these sections are made in three different planes of view: tangential, radial, and transverse (Fig. 5.13).

Tangential sections of wood (Fig. 5.13b) show an end view of the rays. Wood cut in this plane makes interesting grain patterns used in furniture. Radial sections show the rays from a side view (Fig. 5.13c). Transverse sections of wood show an end view of the cells of the axial system (Fig. 5.13d).

Annual rings are concentric rings of cells in the secondary xylem (Figs. 5.12, 5.14). In trees growing in temperate climates, one annual ring forms each growing season. This means that it is usually possible to determine the age of a tree by counting the growth rings. Trees growing in tropical rain forests tend to have irregular growth rings because the climate is always warm and growth happens all during the year. Based on annual ring counts, the oldest known trees--the redwoods (*Sequoia sempervirens*) and bristlecone pines (*Pinus longaeva*)--can be thousands of years old. Additionally, the growth rate of a tree during each growing season can be determined from the thickness of the annual rings. Ecologists use this information to speculate about climate conditions in the past. The study of tree rings is called dendrochronology.



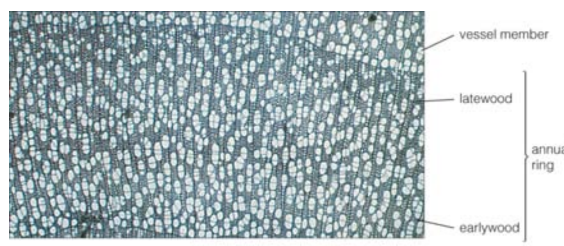


Figure 5.15 (above). Transverse section of diffuse porous wood in elm (*Ulmus* sp.) X57.

Figure 5.14 (left). Section of a 3-year old basswood (*Tillia americana*) stem. X23.

Each annual ring has two components (Fig. 5.14). The cells in the inner part of an annual ring tend to be larger in diameter because they form in the springtime during the first growth spurt of the new season. This is the **springwood** or **earlywood**. The cells that form later in the growing season tend to have smaller diameters. This is the **summerwood** or **latewood**.

One of the structural features used to categorize wood is the distribution of large-diameter vessel members seen in transverse view. In some trees, such as red oak (*Quercus rubra*) (Fig. 5.13), the large-diameter vessel members are located mostly in the springwood. This pattern is called **ring porous**. In other trees, like elm (*Ulmus* sp., Fig.

5.15), the large-diameter vessel members are quite uniformly distributed throughout both the spring- and summerwood, although the cells in summerwood tend to be slightly smaller in diameter. This pattern is called **diffuse porous**.

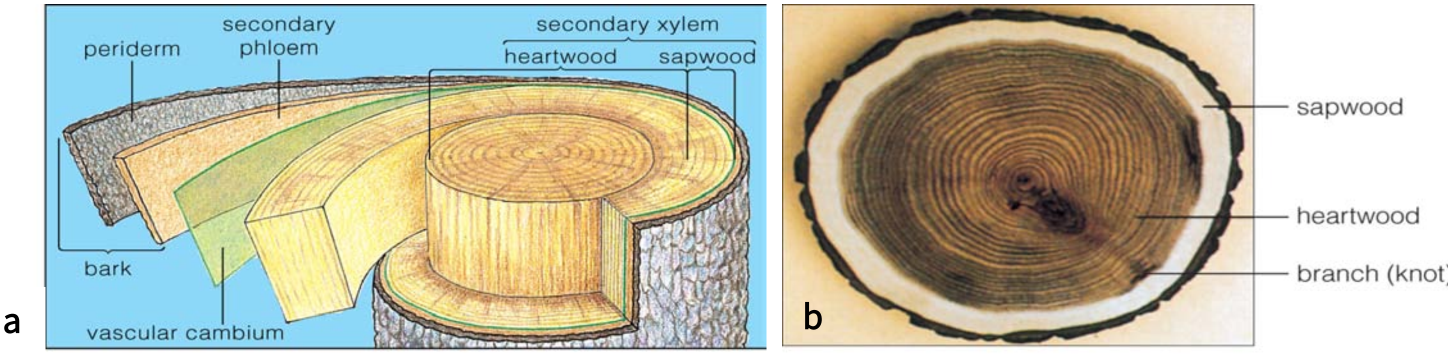


Figure 5.16. (a) Diagram showing the sapwood, heartwood and other components of a woody stem. (b) Slice of a woody stem of mulberry branch (*Morus* sp.) showing the coloration difference between sapwood and heartwood. The dark area from the center to the lower right is an embedded branch that started to grow when this stem was small. This embedded branch will make a "knot" in a board made from this part of the stem.

If you have ever cut down a tree, you may have noticed that the wood in the center of the tree is often darker than the wood near the periphery (Fig. 5.16). The lighter wood near the periphery is called **sapwood**. The secondary xylem cells in this part of the stem are the functioning xylem cells. This is where most of the actual transport of water and dissolved minerals takes place. The darker wood in the center is called **heartwood**. These cells are often filled with resin and other materials that block them, so that they no longer transport. In some woody plants, heartwood vessel members are blocked by structures called *tyloses*. This is true of white oak (*Quercus alba*), the wood used to make wine barrels. In some wood, parenchyma cells lie adjacent to vessel members. A tylose forms when the cell wall of the parenchyma cell actually grows through a pit and into the vessel member. Tyloses look like bubbles; they can fill a vessel member and completely block it (Fig. 5.17).

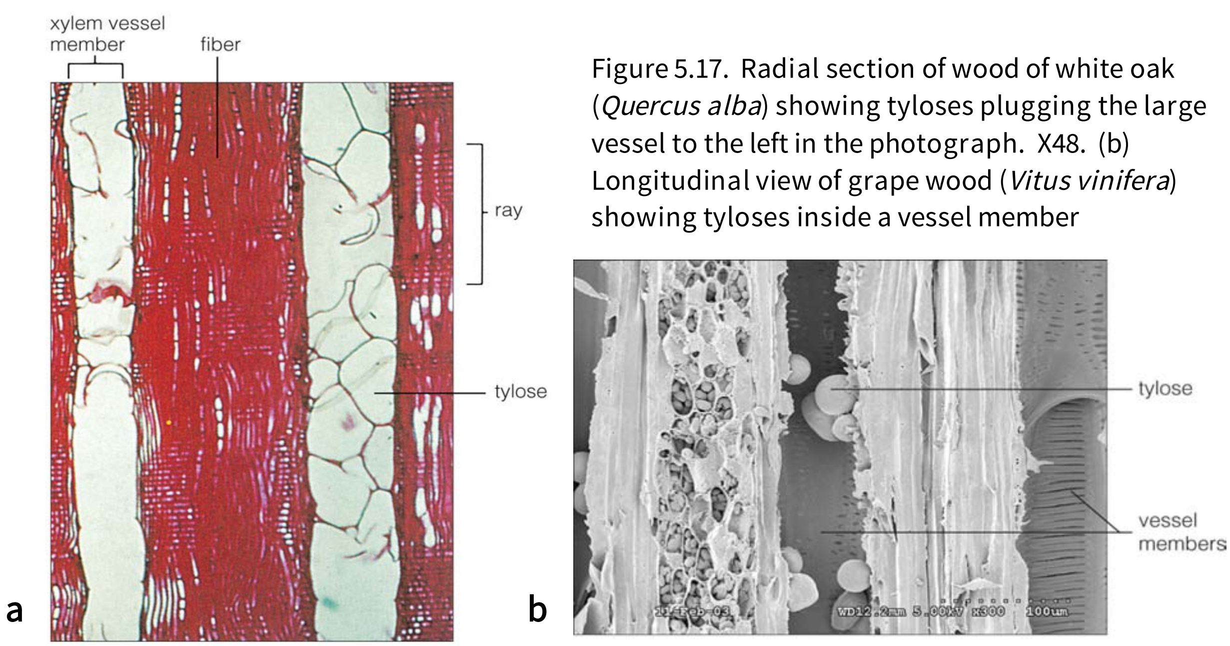
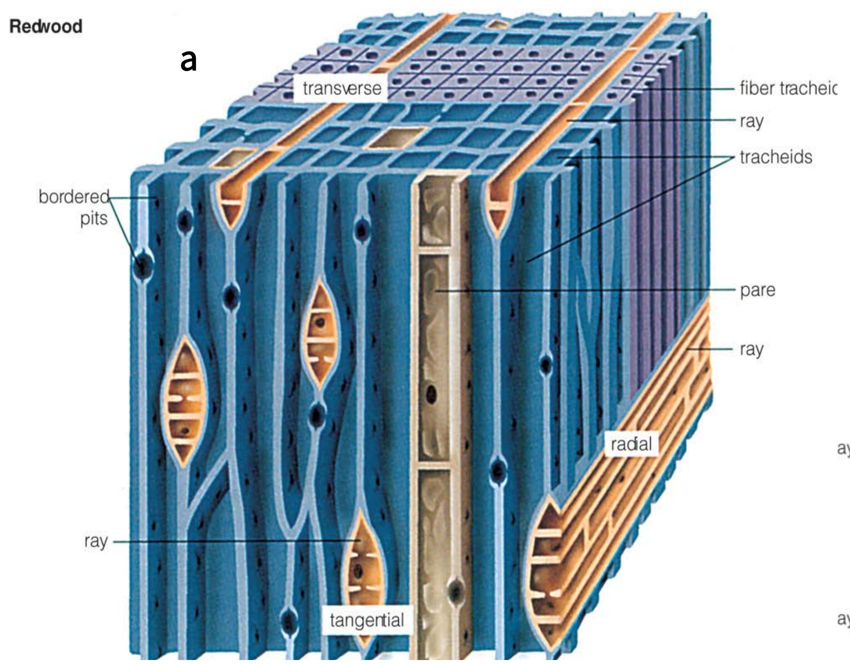


Figure 5.17. Radial section of wood of white oak (*Quercus alba*) showing tyloses plugging the large vessel to the left in the photograph. X48. (b) Longitudinal view of grape wood (*Vitus vinifera*) showing tyloses inside a vessel member

Take one last look at Figure 5.16. Note the dark region labeled "branch (knot)" to the lower right of the image. If a branch forms early in the life of a tree it will be connected at a growth ring near the middle of the stem axis. As the stem continues to enlarge, it gets wider as it forms more and more growth rings. This new growth embeds the base of old branches. When these are cut through to make boards they will be the knots that I'm sure you've seen many times.

Gymnosperm Wood Differs from Angiosperm Wood

The wood we've described is angiosperm (flowering plants) wood: hardwoods such as oak (*Quercus*), elm (*Ulmus*), and walnut (*Juglans*). Gymnosperm (seed plants that do not form flowers; see Ch. 24) wood includes softwoods such as pine (*Pinus*), fir (*Abies*), and redwood (*Sequoia*). It has a simpler structure than angiosperm wood. Angiosperm wood is composed of several different types of cells, which may provide interesting and highly valued grain patterns; gymnosperm wood is composed of only a few cell types, mostly tracheids in the axial system, and very simple rays. A popular wood for building is the redwood (*Sequoia sempervirens*). This wood (shown in tangential, radial, and transverse views in (Figure 5.18) is quite simple in structure. For example, in Figure 5.18d, the annual rings of a redwood tree are apparent, and indeed they are all tracheids. Annual rings can be discerned because the springwood cells are a little wider than the summerwood cells.



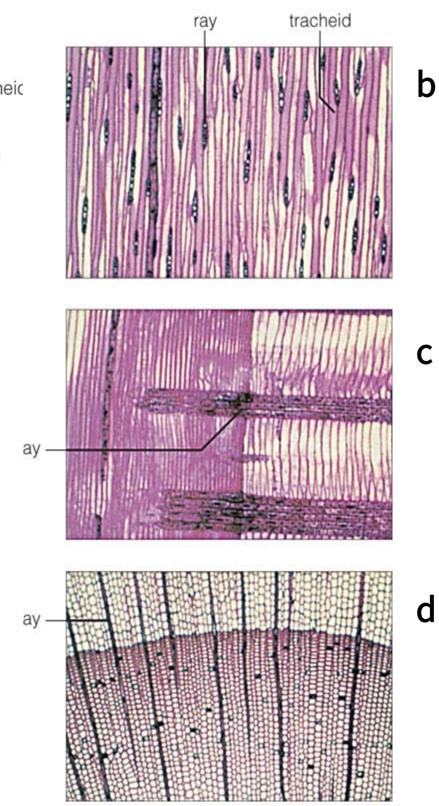


Figure 5.18. Redwood (*Sequoia sempervirens*) secondary xylem. (a) Three-dimensional diagram. (b) Tangential section. (c) radial section. (d) Transverse section. X17.

Some gymnosperm wood have resin ducts (Fig. 5.19), which are secretory structures that produce and transport resin. The resin is synthesized and secreted by a lining of *epithelial cells*. Turpentine is one commercial product made from it. Resin has several names: it is called *sap* when it flows through the resin ducts all the way to the outside of the stem; but when it hardens, it is called *rosin*. Fossilized rosin is the *amber* popular for jewelry. Insects can get stuck in sap, which is why trapped insect bodies are sometimes found in amber.

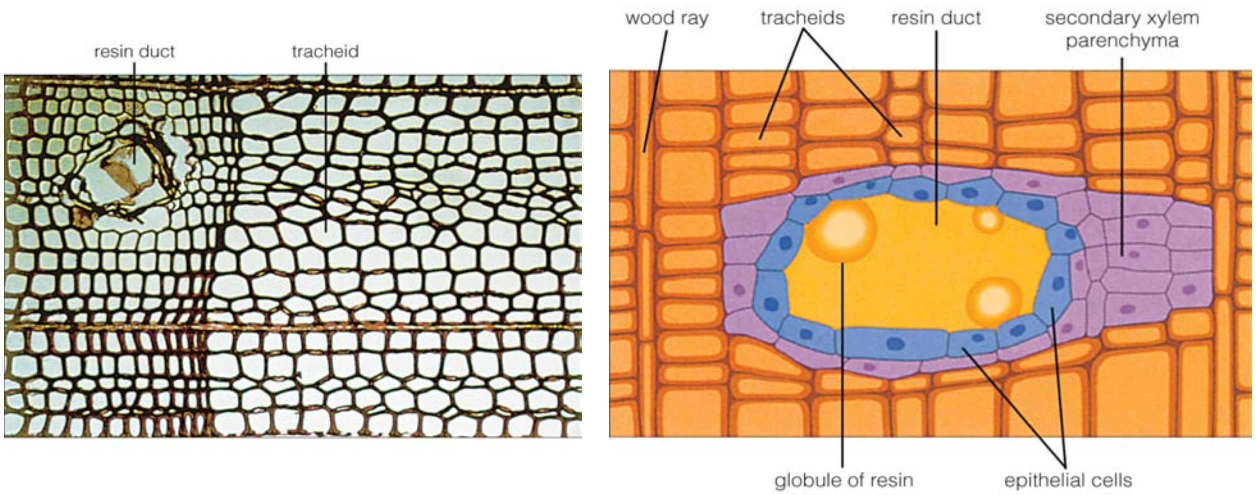


Figure 5.19. (left) Pine wood (*Pinus* sp.) transverse section showing a resin duct. X118. (right) Diagram of a pine wood resin duct showing the secretory cells and globules of resin.

Bark Is Composed of Secondary Phloem and Periderm

The protective covering over the wood of a tree is commonly called bark. In botanical terms, the bark is everything between the vascular cambium and the outside of the woody stem. The actual composition of the bark varies a little, depending on the age of the tree. The bark of a one- or two-year-old tree includes the secondary phloem, maybe a few cells of the cortex, and one or two increments of **periderm**. In a very old tree, the bark would include the layers of secondary phloem plus several layers of periderm (see Fig. 5.16).

SECONDARY PHLOEM **Secondary phloem** (see Fig. 5.14) forms to the outside of the vascular cambium. The types of cells in the secondary phloem are sieve-tube members, companion cells, phloem parenchyma, phloem fibers, sclereids in the axial system, and ray parenchyma in the ray system. When secondary phloem is examined in radial, tangential, and transverse sections, its cellular orientation is similar to that in wood (xylem). A difference in transverse section is that secondary phloem doesn't develop in annual ring increments. You can't count phloem rings to determine tree age (Fig. 5.14). Phloem rays are composed of phloem ray parenchyma cells. Some trees, like basswood (*Tilia americana*) (Fig. 5.14), have wedge-shaped areas of the secondary phloem, called dilated rays , which are composed mostly of secondary phloem ray parenchyma cells.

PERIDERM Usually, stems of plants that live more than one year will lose their epidermis sometime during the first or second year of growth. As the stem increases in diameter because of secondary growth from the vascular cambium, the cells of the epidermis stretch but cannot keep up with the increasing circumference. Eventually, the epidermis cracks, dries up, and flakes away from the stem.

At the same time, some cells (usually in the outer cortex) start to divide all around the periphery of the stem (Fig. 5.20). This new layer of dividing cells is the **cork cambium** (or **phellogen**). The cork cambium divides in two directions, to form **phellem** cells (also called cork cells) to the outside and **phelloderm** cells to the inside.

These three layers--the phellem, the cork cambium, and the phelloderm--make up the periderm (Fig. 5.20c). Phellem cells form in regular rows, have waxy (suberized) cell walls, and are usually dead by the time the periderm is fully functional. The phelloderm cells also form in regular rows, but these cells tend to live longer and look like parenchyma cells. The function of the periderm is to serve as an impermeable layer, inhibiting water evaporation from the protected cell layers and protecting against insect and pathogen invasion.

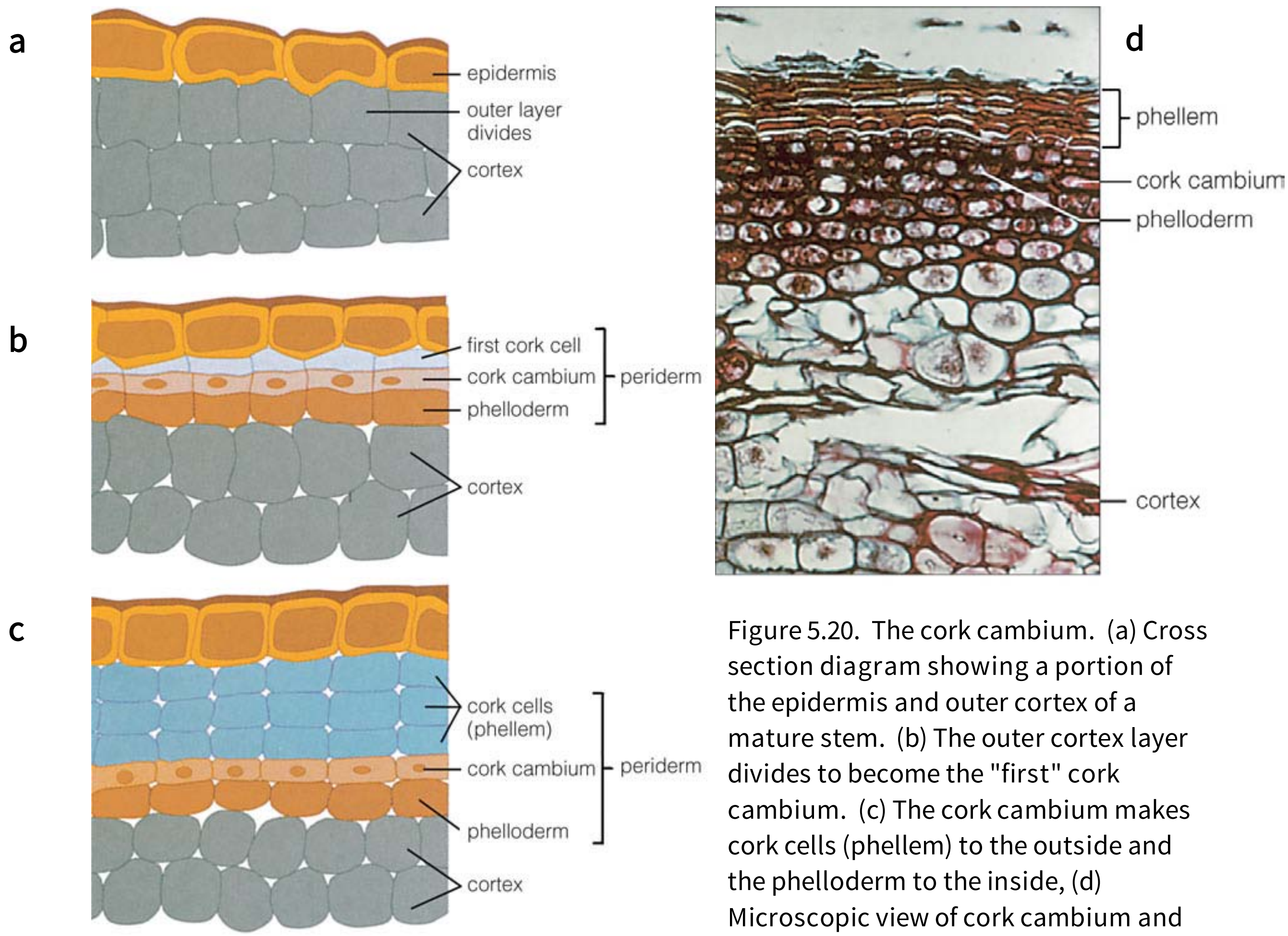


Figure 5.20. The cork cambium. (a) Cross section diagram showing a portion of the epidermis and outer cortex of a mature stem. (b) The outer cortex layer divides to become the "first" cork cambium. (c) The cork cambium makes cork cells (phellem) to the outside and the phelloderm to the inside, (d) Microscopic view of cork cambium and periderm layers in elder (*Sambucus* sp.) stem. X200.

The cells near the surface of the stems of young woody trees are often living. These cells require oxygen to function. Consequently, a structure called a **lenticel** is present in the bark of young branches of different woody plants (Fig. 5.21). Lenticels are specialized regions of the periderm consisting of loosely packaged parenchyma cells. Their purpose is to provide a place where gases can be exchanged.

At the start of each new growing season, a new increment of periderm is initiated. This means that in most trees an entirely new cork cambium is generated each spring. This new cork cambium is initiated from secondary phloem parenchyma cells, which are triggered to divide much like the outer cortex cells that divided to form the first increment of cork cambium. The consequence of this is that the one year's periderm stacks on another, forming layers (Fig. 5.22).

There are always exceptions to the rule, and cork oak (*Quercus suber,* Fig. 5.23a) is one. Instead of new cambium being generated yearly, a single cork cambium lasts the entire life of the tree. Interestingly, it divides only to the outside to form cork cells. Sheets of cork are harvested every 8-10 years for the manufacture of corks for wine bottles and other things. Natural cork is increasingly rare and consequently many wine makers are now using artificial corks for wine bottles.

In bark, the innermost periderm layer is the current active layer. *Girdling,* the removal of a continuous strip of bark around the circumference of a tree, is a sure way to kill it. That's because the nutrient-transporting secondary phloem tissue will be severed.

The external appearance of bark varies among species of trees. Most species can be recognized by their external bark texture (Fig. 5.23). There are several main patterns of bark. The ring bark of, for example, paper birch trees (*Betula papyrifera*), forms in continuous rings (Fig. 5.23b). Scale bark, which is characteristic of pine trees, forms as small overlapping scales (Fig. 5.22). Shag bark, such as that found in *Eucalyptus,* has long overlapping thin sheets (Fig. 5.23c). There are also intermediate forms that are useful for tree identification.

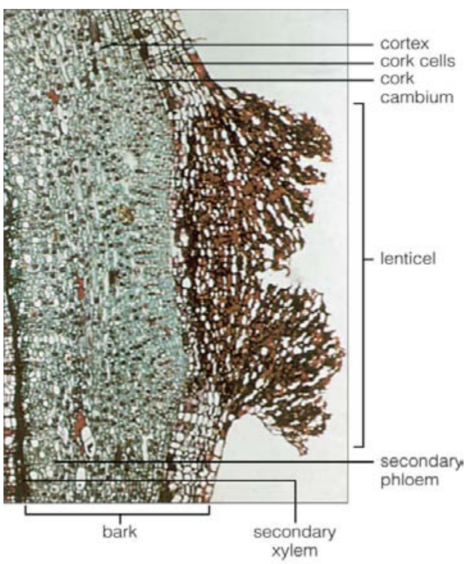
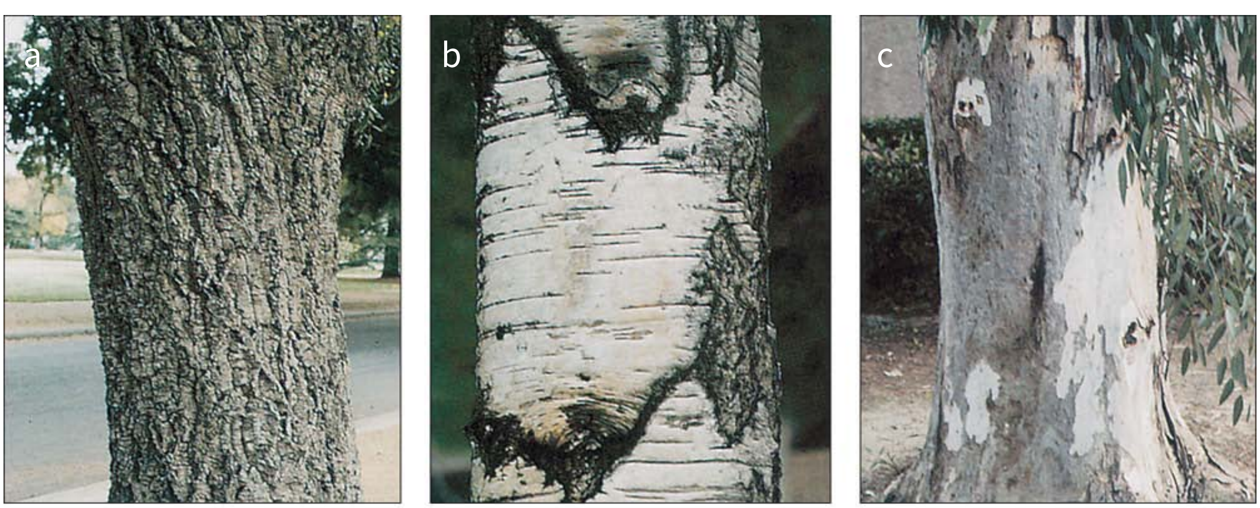


Figure 5.21 (left) Transverse section of a woody stem of elder (*Sambucus* sp.) X83.

Figure 5.22 (above) Bark of pine (*Pinus* sp.) showing layers.

Figure 5.23. (below) Bark of (a) cork oak (*Quercus suber*) (b) birch (*Betula papyifera*), and (c) *Eucalyptus* sp.



Buds Are Compressed Branches Waiting to Elongate

The buds at the ends of woody branches are actually short compressed branches. These buds are covered with several hard, modified leaves called bud scales, which keep the inside of the bud fresh and moist. The bud at the end of a branch is called the terminal bud; those in the axils (at the base of the petiole) of leaves on the side of a branch are called lateral buds (Fig. 5.24). Some buds produce flower parts instead of leaves; these are called flower buds. In some fruit trees, like almonds and apricots (both *Prunus* sps.), the first buds to open in the spring are flower buds.

When a bud elongates, as in the early spring, the bud scales open and finally fall off, leaving small scars called bud-scale scars. When a leaf falls, it leaves a leaf scar (Figs. 5.24, 5.25). The vascular bundles that pass through the leaf into the stem also break off when the leaf falls, these scars are called bundle scars. The structure of the leaf scar and the number and distribution pattern of the bundle scars are characteristic of the plant and can be used to identify plants in the winter when all their leaves have fallen (Fig. 5.25).

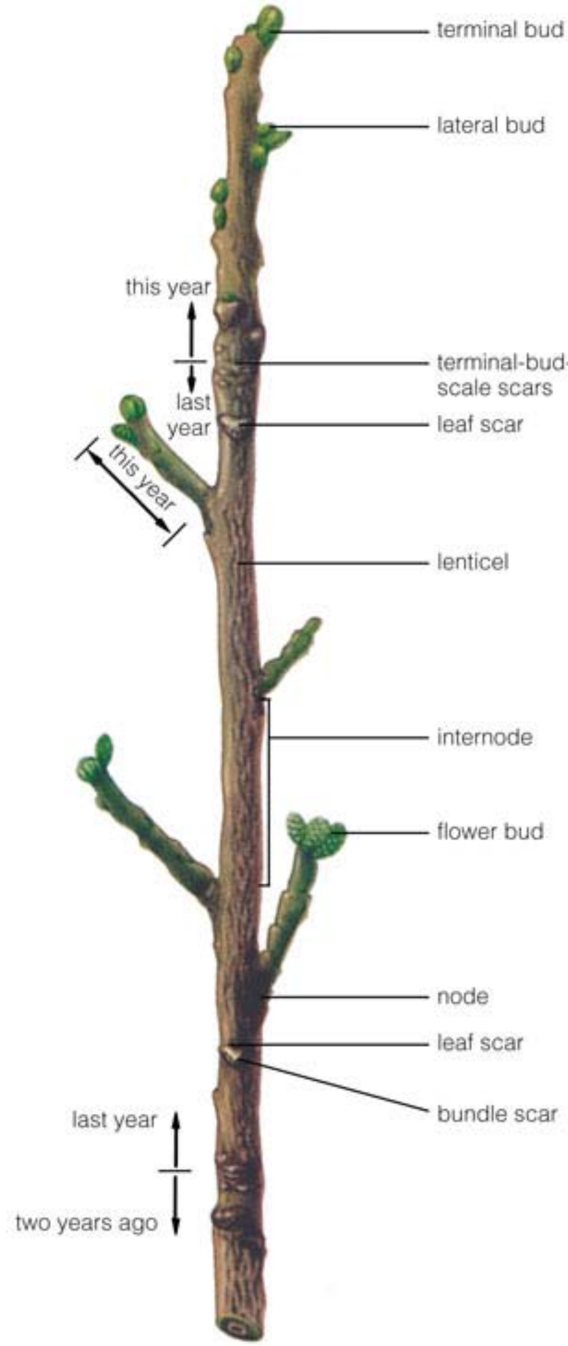


Figure 5.24 (above). Three-year-old twig of walnut (*Juglans regia*).

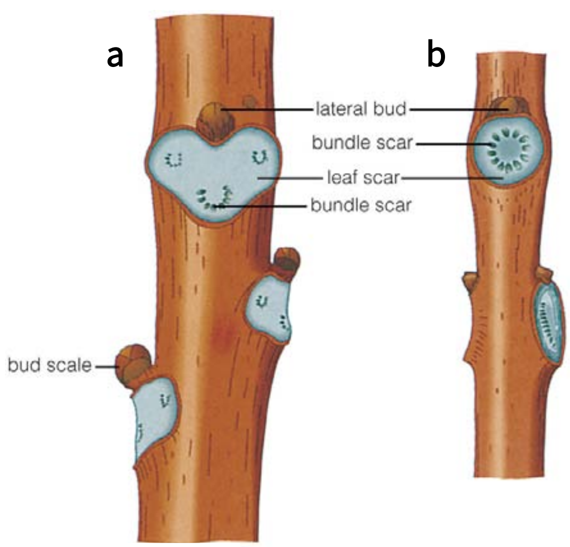


Figure 5.25 (left). Leaf scars and buds. (a) Walnut (*Juglans regia*); (b) catalpa (*Catalpa bignonioides*).

Some Monocot Stems Have Secondary Growth

Most monocots lack a vascular cambium and do not form secondary xylem and phloem. Such plants cannot support large vertical shoot systems. Other monocots such as different types of lilies (*Lilium* sp.) can become very large plants by producing elaborate underground branches (rhizomes).

Treelike monocots (Fig. 5.26), such as coconut trees (*Cocos* sp.) and Joshua trees (*Yucca brevifolia*), can reach enormous size. There are actually three different types of monocot tree: (1) palms, such as the coconut tree, which are unbranched and do not have true secondary growth (Fig. 5.26a); (2) pandans (*Pandanus* sp.), which have branched stems but also lack true secondary growth (Fig. 5.26b); and (3) tree lilies (such as *Yucca*) and others (Fig. 5.26c), which have branches, a cambium, and true secondary growth.

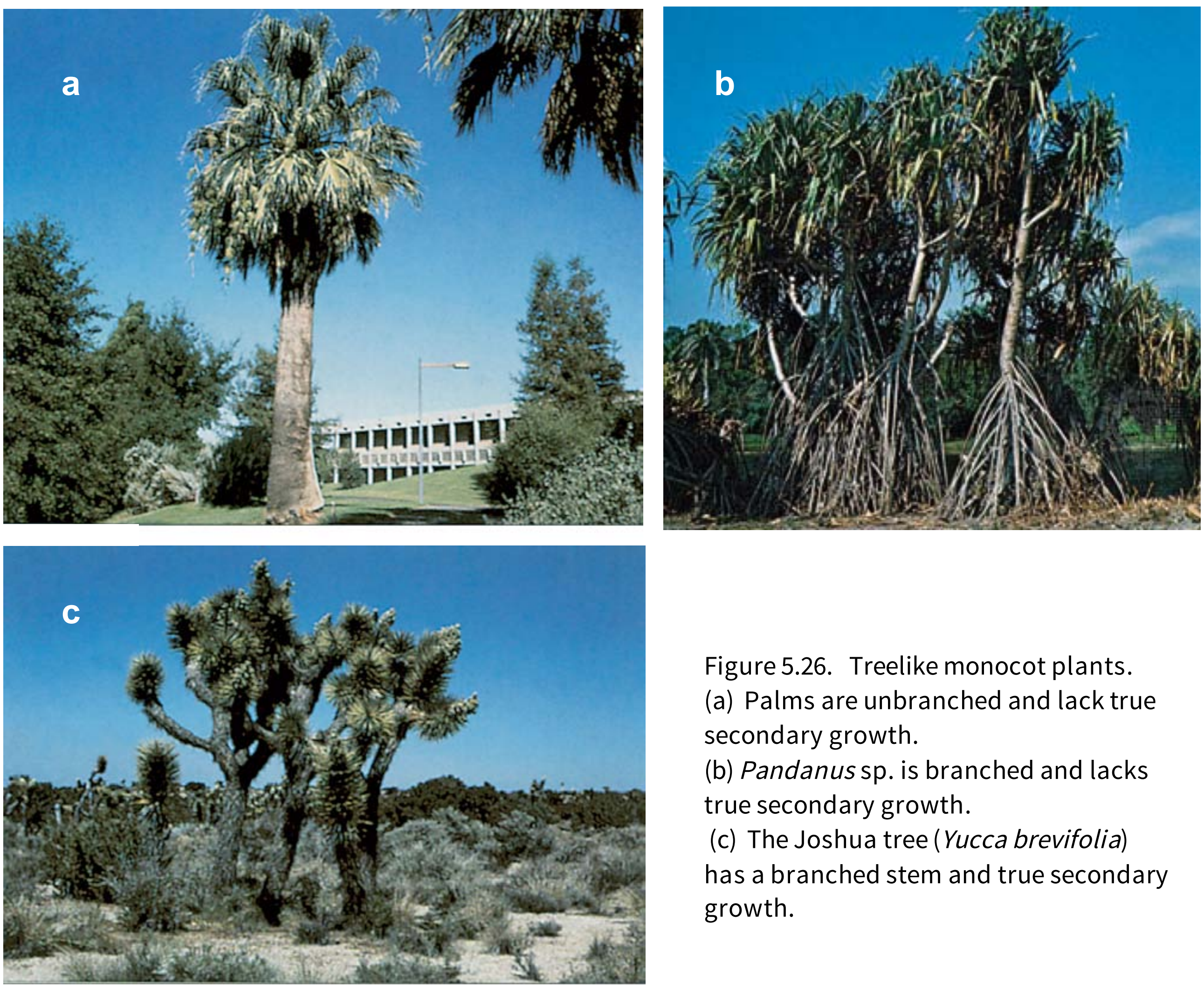


Figure 5.26. Treelike monocot plants.
(a) Palms are unbranched and lack true secondary growth.
(b) *Pandanus* sp. is branched and lacks true secondary growth.
(c) The Joshua tree (*Yucca brevifolia*) has a branched stem and true secondary growth.

Palm stems have a very large number of vascular bundles, most of which are leaf traces. The leaves are large, and the leaf base wraps around the stem. Each leaf has many leaf traces. Some thickening does occur at the bases of palms, but this comes from basal adventitious roots (look at the very bottom of the palm tree in figure 5.26a). Some thickening throughout the stem results from the division and enlargement of parenchyma cells; this is called *diffuse secondary growth*. It isn't true secondary growth because a cambium is lacking.

Several monocot plants, including *Yucca, Agave* (century plant), and *Dracaena* (dragon's blood tree), have true secondary growth from a cambium. The stems of these plants are tapered: thin at the top and thick at the base. This architecture results from the pattern of cells the cambium produces. The monocot cambium is unique in forming mostly parenchyma cells with secondary vascular bundles embedded in this ground tissue (Fig. 5.27). The secondary vascular bundles are different from primary vascular bundles in that the xylem surrounds the phloem.

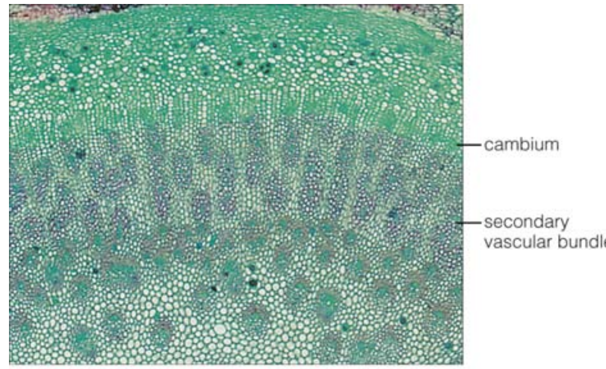


Figure 5.27. Transverse section of Dragon's Blood Tree (*Dracena draco).*
The cambium layer produces secondary vascular bundles and parenchyma cells. X12.

Some older monocot stems have a corklike layer that replaces the epidermis. This layer, called *storied cork*, isn't considered to be periderm because no cork cambium is present. Storied cork forms by the division of parenchyma cells along the stem periphery.

5.4 STEM MODIFICATIONS FOR SPECIAL FUNCTIONS

Stems of both dicots and monocots may be adapted for functions other than support, transport, and the production of new growth. They may, for instance, serve as protective devices or as attachment organs for vines, carry on photosynthesis, or store food or water.

Rhizomes are underground stems (Fig. 5.28a). They are usually light colored and burrow into the ground just below the surface. In some plants, such as bermuda grass (*Cynodon dactylon*), the rhizomes can be quite deep--40 cm (16 in) or so. Since rhizomes are modified stems, they have internodes and nodes. Small scalelike leaves sometimes form at the nodes, but they don't grow or become photosynthetic. The buds in the axils of these scale leaves elongate, producing new branches that extend to the soil surface and form new plants.

Tubers are the enlarged terminal portions of underground rhizomes. The potato plant (*Solanum tuberosum*) has three types of stems: (1) upright leafy stems; (2) underground rhizomes; and (3) swollen ends of rhizomes, the tubers (Figs. 5.28b, 5.29a). The structure of a tuber shows it to be a stem. The eyes of a tuber are actually lateral buds formed in the axil of small scale leaves at a node. The internodes of the tuber are short, and the tuber body is filled with parenchyma cells containing starch, a storage form of sugar.

Corms and bulbs are shoot structures modified for storage of food. A **corm** is a short, thickened underground stem with thin, papery leaves. *Gladiolus* sp. corms are good examples. The central portion of the corm accumulates stored food, which is used at the time of flowering (Fig. 5.28c). New corms can form from the lateral buds on the main corm. A **bulb** differs from a corm in that the food is stored in specialized fleshy leaves (Fig. 5.28d). The stem portion is small and has at least one terminal bud (to produce a new, upright leafy stem) and a lateral bud (to produce a new bulb). Food stored in the bulb is used up during the initial growth spurt each spring. A table onion (*Allium cepa*) is an example of a bulb.

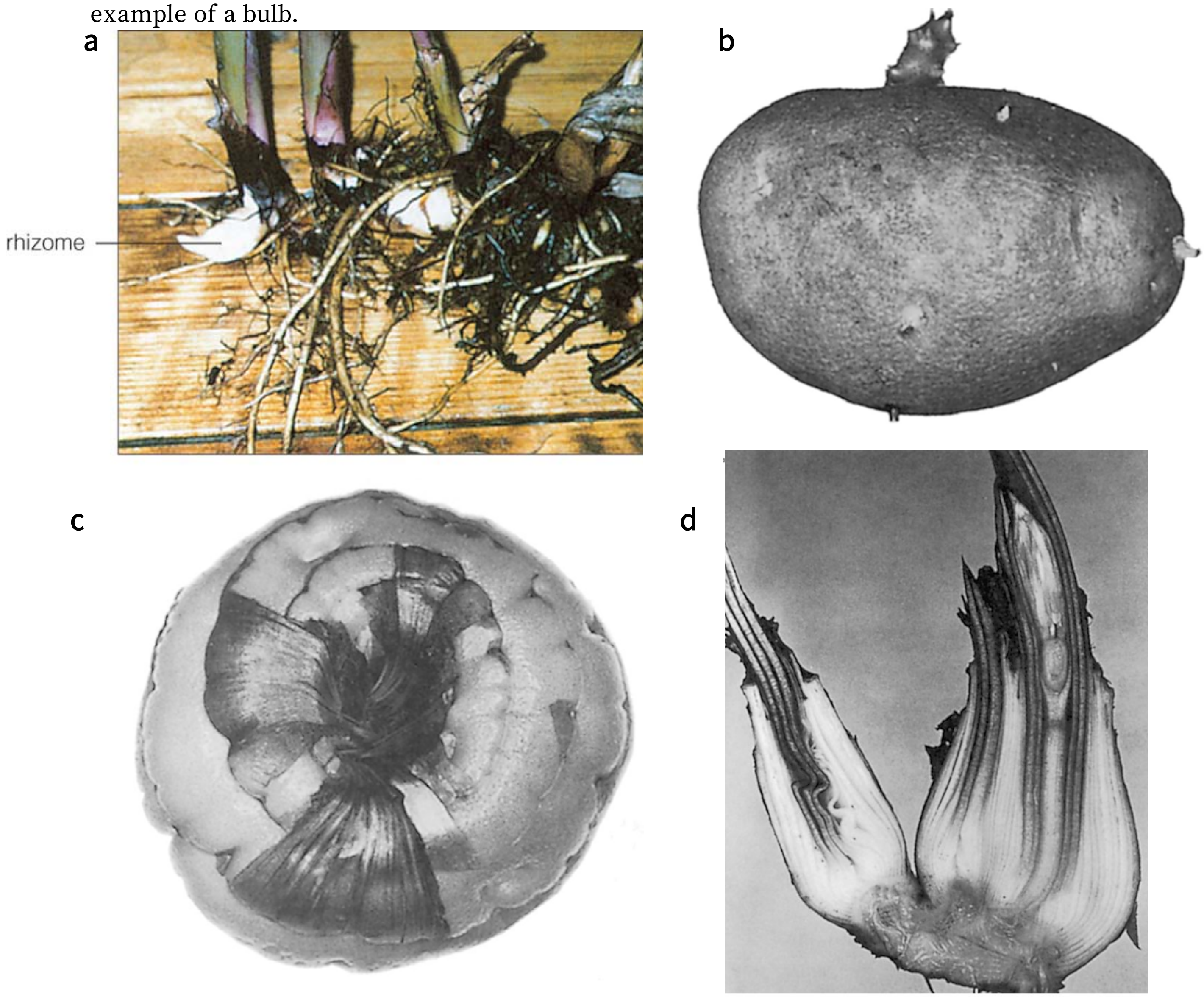


Figure 5.28. Specialized stems. (a) Rhizome of *Canna* lily; (b) Potato tuber (*Solanum tuberosum*); (c) top view of corm in *Gladiolus*; (d) Split view of a daffodil (*Narcissus*) bulb showing short stem and thick fleshy leaves.

Cladophylls (also called cladodes) are flattened photosynthetic stems that function as and resemble leaves. They are not actually leaves in a developmental sense, because they develop from buds in the axils of small, scalelike leaves. Cladophylls may bear flowers, fruits, and small leaves. Butcher's broom (*Ruscus aculeatus*, Fig. 5.29b), asparagus, and some cacti are examples of plants with cladophylls.

Thorns originate from the axils of leaves (Fig. 5.29c) and help protect the plant from predators. Some thorns actually have leaves growing on them. From developmental evidence, we know that prickles and spines (though outwardly similar structures) are not modified stems. Spines are actually modified leaves; prickles, like those on rose stems, are really modified clusters of epidermal hairs.

Stolons, also called *runners*, are aboveground horizontal stems. Strawberry plants (*Fragaria* sp.) send out stolons (Fig. 5.29d). At each node of the stolon, a small leaf will form, and in its axil a root and a bud will sprout to initiate a new strawberry plant. The stolon helps the plant spread. Some successful weed plants, like Bermuda grass, also can spread by stolons.

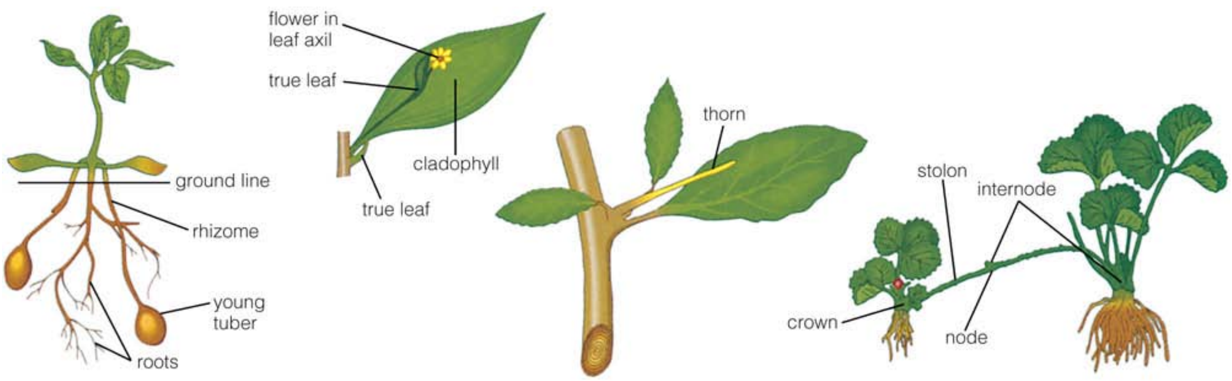


Figure 5.29. Stem modifications. From left to right: A young potato plant (*Solanum tuberosum*) showing development of young tubers developing at the ends of rhizomes. Cladophyll in butcher's broom (*Ruscus aculeatus*). Thorn growing from the axil of a *Pyracantha* sp. leaf. Stolon in strawberry (*Fragaria* sp.).

5.5 THE ECONOMIC VALUE OF WOODY STEMS

Trees are, without doubt, among the most valuable things on earth. Our forests are home to countless plants and animals. They are also a source of the raw material for many useful products. They purify our air, keep our soil from washing away, and affect our weather patterns. The implications of the loss of our forests are too terrible to consider. We must be extremely careful to protect and manage this natural resource even as we grow and harvest woody plants for thousands of uses.

Trees are grown for wood; for sugar (from maple trees, *Acer saccharum*); and for secondary products such as turpentine (from the pine, *Pinus palustris*), natural rubber (from the Brazilian rubber tree, *Hevea brasiliensis*), and chewing gum (from the sapodilla tree, *Achras sapota*). These products are harvested by making cuts in the woody stem and collecting the sap that runs out (Fig. 5.30). The raw secondary product is then processed to make commercially important materials. This is a truly renewable resource because the trees can live and continue to produce for many years.

Figure 5.30. Maple syrup being harvested from sugar maple trees (*Acer saccharum*).

In contrast, when trees are used for lumber they are destroyed. In the manufacture of lumber, a tree is removed from the forest with large machines and trucked or floated down a river to a sawmill. The log is moved to the mill and oriented so that tangential cuts are made along its length to make boards (Fig. 5.31a). Different types of wood grain can be obtained, depending on the type of cut made and on the quality and type of wood used.

Sheets of plywood are made by steaming the log and then placing it against a large lathe that literally peels thin sheets of wood from the slowly revolving log (Fig. 5.31b). The sheets are then cut to size, and multiple sheets are glued together to make plywood of the desired thickness.

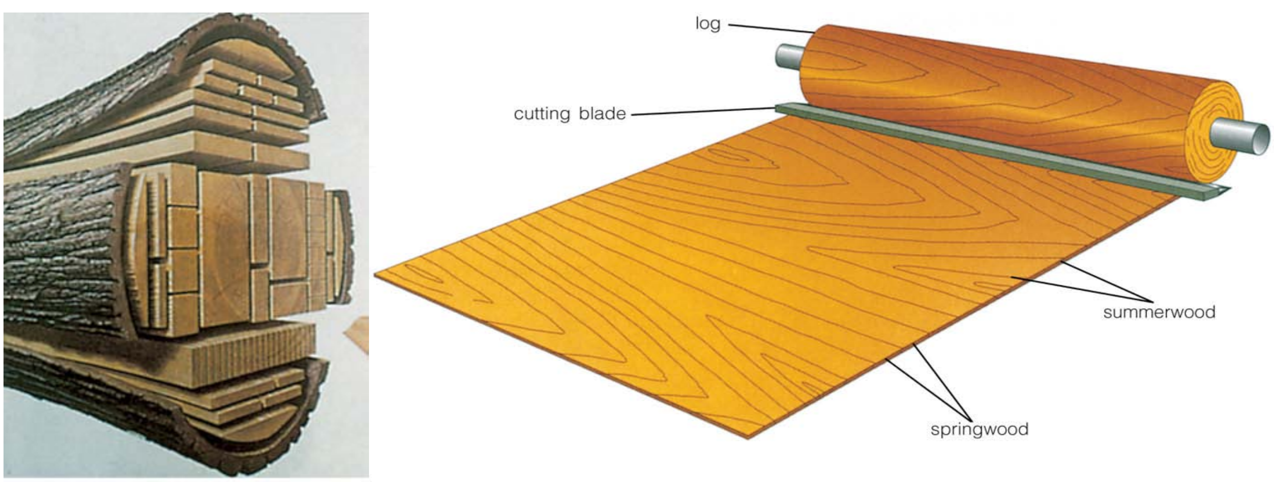


Figure 5.31. (left) Diagram showing the different cuts of a log. (right) Diagram showing a sheet of plywood being peeled from a slowly revolving log.

For other industrial uses, wood is not sawed into boards or cut into sheets, but broken down by machines into individual fibers, tracheids, and vessel members. This pulp is then processed to make paper and cardboard products. In papermaking, the lignin in the secondary cell walls is removed. In the past such waste products have caused environmental pollution. Recently, innovative products, including soil conditioners and adhesives, have been developed using these wastes .

Recycling paper products is now a major activity, and this important practice means that our natural tree resources may be preserved for many generations to come. Processing recycled paper is not without its hazards; it releases vast quantities of toxic inks and chemicals used in printing. Intelligent processing, however, has resulted in the discovery of ways to detoxify and reuse these materials.

KEY TERMS

axial system;
bulb
cladophylls
cork cambium
corm
diffuse porous
earlywood
fascicular cambium
fusiform initials
heartwood
interfascicular cambium
latewood
lenticels
periderm
phellem
phelloderm
phellogen
primary thickening meristems
ray initials
ray system
rhizomes
ring porous
sapwood
secondary phloem
secondary xylem
springwood
stolons
summerwood
thorns
tubers
vascular cambium

SUMMARY

1. The functions of stems are: (a) to provide the axis for the attachment of the leaves, buds, and flowers; (b) to provide pathways for movement of water and minerals from the roots and food from the leaves; and (c) to produce new cells, tissues, leaves, and buds.

2. The shoot apical meristem forms the three primary meristems: protoderm, procambium, and ground meristem.

3. Bundles of procambium form in a ring pattern (in dicot stems) between the two parts of the ground meristem (which will become the pith and cortex). In monocot stems the bundles are scattered throughout the ground tissue, and the terms pith and cortex are usually not used. Procambium cells will become primary xylem and phloem.

4. Leaves are arranged on the stem according to four basic patterns (phyllotaxis): alternate, opposite, whorled, and spiral.

5. The vascular cambium in dicot stems forms from the fascicular cambium (by division of residual procambium cells within the vascular bundles) and from the interfascicular cambium (by division of parenchyma cells between vascular bundles).

6. Cells in wood are arranged into axial and ray systems. The cells of the axial system come from fusiform initials in the vascular cambium; those of the ray system come from ray initials.

7. One year's increment of growth in wood produces one annual ring. Cells in earlywood (springwood) have relatively large diameters and form in the spring. Latewood (summerwood) cells form later in the summer and have smaller diameters. Ring porous wood has large vessel members only in the earlywood; diffuse porous wood has large vessel members throughout the annual ring, but the cells in latewood are smaller.

8. Angiosperm wood (hardwood) is more complex anatomically than gymnosperm wood (softwood). Gymnosperm wood is composed mostly of tracheids and simple rays, whereas angiosperm wood is composed of vessel members, tracheids, fibers, parenchyma cells, and more complex rays.

9. The bark consists of all tissues outside of the vascular cambium-- secondary phloem, layer or layers of periderm. Bark occurs in different patterns.

10. The periderm forms from the cork cambium by divisions of outer cortex cells. Cork cells form to the outside of the cork cambium, and phelloderm cells form to the inside. During subsequent years, new layers of periderm are added in the secondary phloem.

11. Different kinds of buds occur on woody stems: terminal buds, lateral buds, and flower buds. Bud scale scars and leaf scars form after bud scales and leaves fall from the stem.

12. Monocot stems have scattered vascular bundles and usually do not have secondary growth. Palm trees increase their thickness by diffuse division of parenchyma cells. Monocot trees, such as *Yucca* and *Dracaena*, have a cambium and true secondary growth with a vascular cambium.

13. Several different modified stems occur in flowering plants: rhizomes, corms, bulbs, tubers, cladophylls, thorns, and stolons are examples.

14. Trees are ecologically essential and provide many products for humans. It is imperative that they be conserved.

Questions

1. Diagram and describe the primary meristems that develop into the primary tissues.

2. Given an illustration of a section of a stem, identify the tissues and cell types present. Also, make a diagram (cross section or longitudinal section) of a stem and label all of the tissues and cell types.

3. Name and describe the four types of phyllotaxis. List one plant of each type found in your area.

4. Describe the initiation of vascular cambium and the formation of secondary xylem and phloem in a stem.

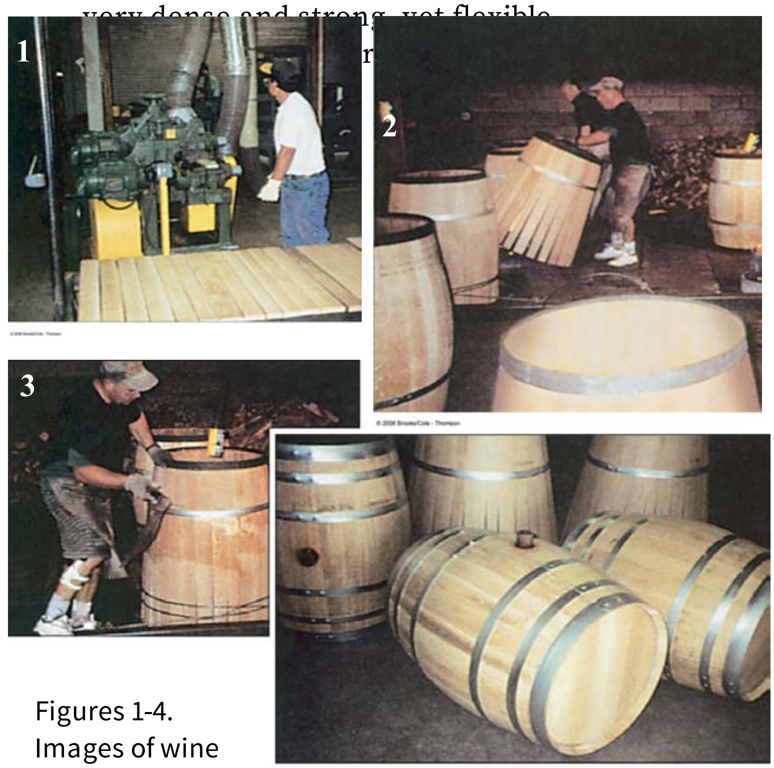
5. Describe the initiation and activity of the cork cambium forming the periderm.

6. How do the stems of monocots and dicots differ anatomically?

ECONOMIC BOTANY: ***How do you make a barrel?***

The highest-quality red wines, as well as chardonnay (a white wine), are carefully aged in oak barrels for several months. Vintners are experts--artists, actually--at selecting the best barrel and at timing the aging process to produce the best-tasting wine. Did you ever wonder where these barrels come from and how they are made? I found out when I visited the Mendocino Cooperage, a barrel-making factory at northern California's Fetzer Winery in Hopland.

No wood is better suited for aging wine than oak--specifically, white oak (*Quercus alba*). If you look at the cellular structure of any species of oak (see Fig. 5.13, red oak), you will see a multitude of wide and short vessel members, surrounded by fibers with thick cell walls, and large, multicellular rays . This combination makes for a wood that is very dense and strong, yet flexible



Figures 1-4. Images of wine barrel making.

Two other features make white oak the wood of choice. One is that the vessel members are plugged by tyloses, the bubble-shaped ingrowths from surrounding parenchyma cells. Tyloses inhibit pathogen movement in inactive wood, and they make white oak wood good for barrels because the tyloses also make the wood leak resistant (see Fig. 5.17). Nothing, including water, can move up a vessel when it is plugged with tyloses; so nothing can leak out of these barrels, either. The other feature is that the cells making up the wood contain many complex chemicals: phenolics (complex polymers of phenol units; phenols are six-carbon ring molecules), carbohydrates, and other carbon compounds that add desirable aromas and tastes to aged wine. These aromas and tastes have become traditional and are expected by wine drinkers.

The best American barrels come from white oak trees grown in the cold climates of Minnesota and Iowa. The wood from these old trees (100 to 200 years old) has tight grain (small annual rings) because the trees grow very slowly and uniformly. The wood is clear and light colored.

Making barrels is a rare and highly valued craft. There are very few master coopers (barrel makers) in the United States. At the beginning of the coopering process, white oak wood is sawn into boards about 1 meter (~39 in) long, a little over 2.5 cm (1 in) thick, and 7.5-12.5 cm (3-5 in) wide. The boards are stacked so that air can circulate among them, and they are aged outside for two years. The boards are then examined one at a time for imperfections, and the perfect ones are planed and trimmed into barrel staves

(Fig. 1). The staves are tapered toward their ends, and their edges are beveled so that they will fit very snugly together when bent.

Each barrel is made of the same number of staves. These are collected together in a steel ring, and a hoop is pushed snugly part way up the forming barrel (Fig. 2). The barrel is then held over a small open flame (Fig. 2) to heat the wood and release whatever water is still left in the cells of the wood. At the same time, a long cable is wrapped around the bottom of the forming barrel (you can see it at the bottom of figure 3). As the barrel continues to heat, the cooper wets the outside. The barrel slowly turns. As the cable pulls tighter, the staves bend and end up tightly pressed together (Fig. 3). After a certain amount of time, the cooper pulls the barrel off the fire and adds a second hoop on the other end. The new barrel is then placed into a machine to even all the staves, and the remaining steel hoops are pounded into position. No screws or nails are used at any step in the process.

The barrel ends are also made of oak-wood pieces. These are fired briefly, sawn to the correct length, and fitted together with wood pegs. Rush leaves are placed between the boards to seal them together. The covers are then pressed together and planed smooth, and an edge is cut all around the cover. The cooper rubs a flour-and-water paste into the groove at the lip of the barrel and hammers the cover into place very cleverly. The barrel is complete (Fig. 4). Barrels are then pressure tested for leaks with water and air. The ends of the staves are examined for water seepage and are plugged if necessary.

New barrels impart a very specific flavor and aroma to the wine. Chardonnay, as an example, will age in oak barrels for seven to eight months. Red wines may be aged longer. A typical barrel loses its characteristic flavor after being used twice. After that, the barrel may be used for several more years to store less vintage wines. A typical wine barrel has a working life of about eight years, after which you may find it cut in half and growing tomatoes in someone's garden. Making good barrels is really an art form. I will look at them with new eyes from now on.

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