Concept 35.2

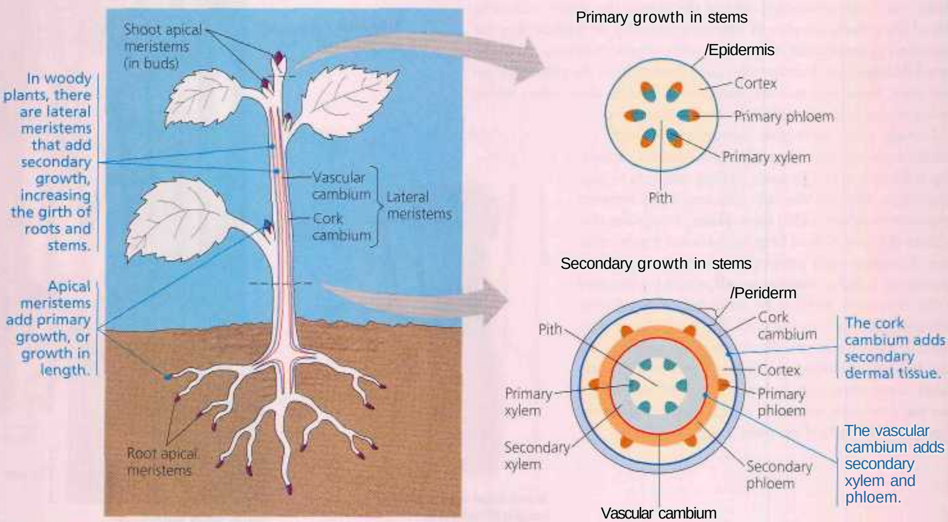
Meristems generate cells for new organs

So far, we have looked at the structure and arrangement of plant tissues and cells in mature organs. But how does this organization arise? A major difference between plants and most animals is that plant growth is not limited to an embryonic or juvenile period. Tnstead, growth occurs throughout the plant's life, a condition known as **indeterminate growth.** At any given time, a typical plant consists of embryonic, developing, and mature organs. Except for periods of dormancy, most plants grow continuously In contrast, most animals and some plant organs, such as most leaves, undergo **determinate growth;** that is, they cease growing after reaching a certain size.

Although plants continue to grow throughout their lives, they do die, of course. Based on the length of their life cycle, flowering plants can be categorized as annuals, biennials, or perennials. **Annuals** complete their life cycle—from germination to flowering to seed production to death—in a single year or less. Many wildflowers are annuals, as are the most important food crops, including the cereal grains and legumes. **Biennials** generally live two years, often including an intervening cold period (winter) between vegetative growth (first spring/summer) and flowering (second spring/summer). Beets and carrots are biennials but are rarely left in the ground long enough to flower. **Perennials** live many years and include trees, shrubs, and some grasses. Some buffalo grass of the North American plains is believed to have been growing for 10,000 years From seeds that sprouted at the close of the last ice age. When a perennial dies, it **is** not usually from old age, but from an infection or some environmental trauma, such as fire or severe drought.

Plants are capable of indeterminate growth because they have perpetually embryonic tissues called meristems. There are two main types; apical meristems and lateral meristems. **Apical meristems,** located at the tips ol roots and in the buds of shoots, provide additional cells that enable the plant to grow in length, a process known as **primary growth.** Primary growth allows roots to extend throughout the soil and shoots to increase exposure to light and CO_2. In herbaceous (nonwoody) plants, primary growth produces all, or almost all, of the plant body Woody plants, however, grow in girth in the parts of stems and roots where primary growth has ceased. This growth in thickness, known as **secondary growth,** is caused by the activity of **lateral meristems** called the vascular cambium and cork cambium. These cylinders of dividing cells extend along the length of roots and stems **(Figure 35.10).** 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.

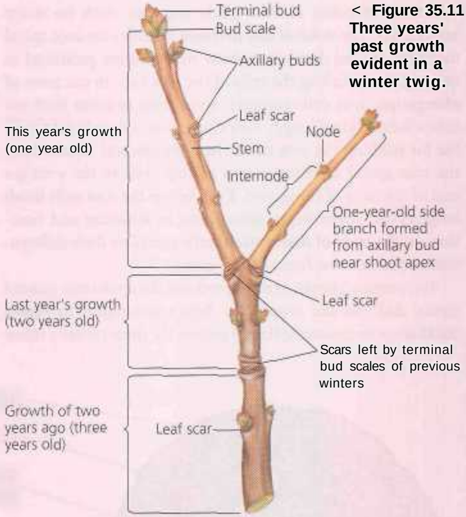
The ceils within meristems divide relatively frequently, generating additional cells. Some products of this division



▲ Figure 35.10 An overview of primary and secondary growth.

remain in the meristem and produce more cells, while others differentiate and are incorporated into tissues and organs of the growing plant. Cells that remain as sources of new cells are called initials. The new cells displaced from the meristem, called derivatives, continue to divide until the cells they produce become specialized within developing tissues.

In woody plants, primary and secondary growth occur simultaneously but in different locations. Each growing season, primary growth near the apical meristems produces young extensions of roots and shoots, while lateral meristems produce secondary growth that thickens and strengthens older parts of the plant **(Figure 35.11).** The oldest regions, such as a tree trunk base, have the most accumulation of tissues produced by secondary growth.



< Figure 35.11 Three years' past growth evident in a winter twig.

Concept Check 35.2

1. Cells in lower layers of your skin divide and replace dead cells sloughed from the surface. Why is it inaccurate to compare such regions of cell division to a plant meristem?
2. Contrast the types of growth arising from apical and lateral meristems.

For suggested answers, see Appendix A.

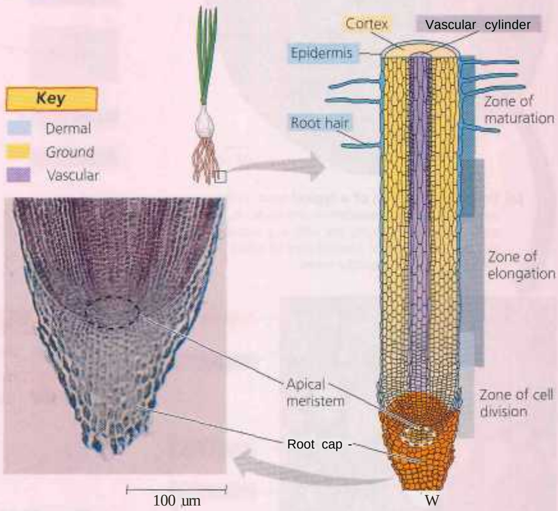
Concept 35.3

Primary growth lengthens roots and shoots

Primary growth produces the primary plant body, the parts of the root and shoot systems produced by apical meristems. In herbaceous plants, the primary plant body is usually the entire plant. In woody plants, it consists only of the youngest parts, which have not yet become woody. Although apical meristems lengthen both roots and shoots, there are differences in the primary growth of these two systems.

Primary Growth of Roots

The root tip is covered by a thimble-like root cap, which protects the delicate apical meristem as the root pushes through the abrasive soil during primary growth. The root cap also secretes a polysaccharide slime that lubricates the soil around the root tip. Growth occurs just behind the root tip, in three zones of cells at successive stages of primary growth. Moving away from the root tip, they are the zones of cell division, elongation, and maturation **(Figure 35.12).**



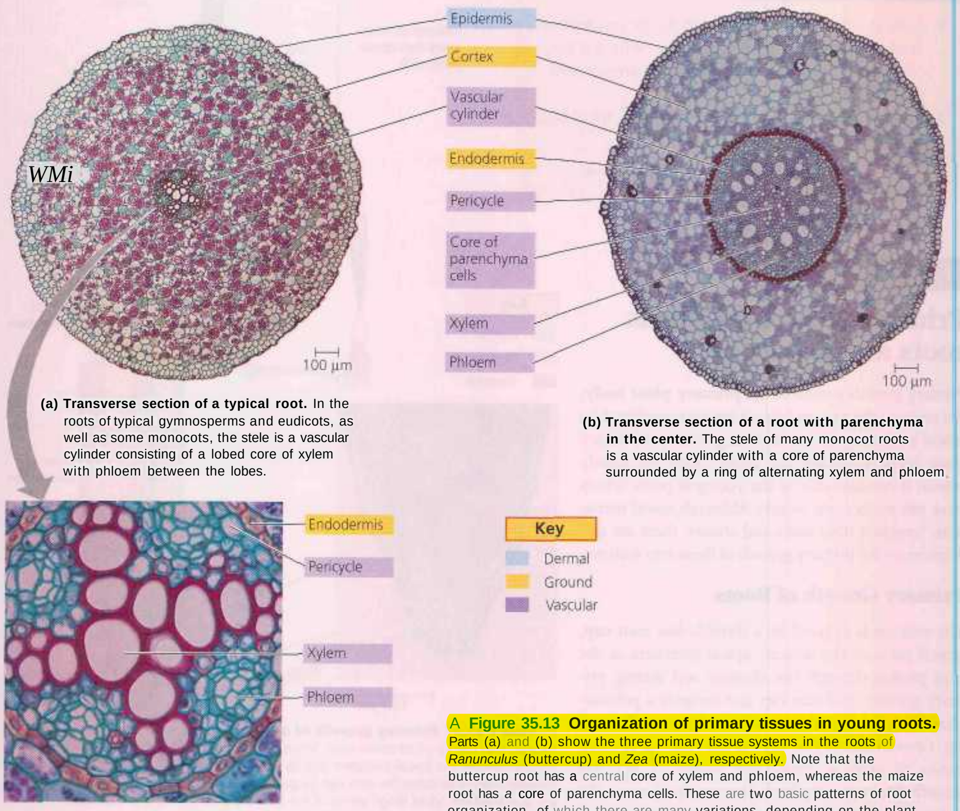
▲ Figure 35.12 Primary growth of a root. The diagram and light micrograph take us into the tip of an onion root. Mitosis is concentrated in the zone of cell division, where the apical meristem and its immediate products are located. The apical meristem also maintains the root cap by generating new cells that replace those that are sloughed off. Most lengthening of the root is concentrated in the zone of elongation. Cells become functionally mature in the zone of maturation. The zones grade into one another without sharp boundaries.

The three zones of cells grade together, with no sharp boundaries. The **zone of cell division** includes the root apical menstem and its derivatives. New root cells are produced in this region, including the cells of the root cap. In the **zone of elongation,** root cells elongate, sometimes to more than ten times their original length. Cell elongation is mainly responsible for pushing the root tip farther into the soil. Meanwhile, the root apical meristem keeps adding cells to the younger end of the zone of elongation. Even before the root cells finish lengthening, many begin specializing in structure and function. In the zone of **maturation,** cells complete their differentiation and become functionally mature.

The primary growth of roots produces the epidermis, ground tissue, and vascular tissue. The light micrographs in **Figure 35.13** show in transverse (cross) section the three primary tissue systems in the young roots of a eudicot *(Ranunculus,* buttercup) and a monocot *(Zea,* maize). Water and minerals absorbed from the soil must enter through the epidermis, a single layer of cells covering the root. Root hairs enhance this process by greatly increasing the surface area of epidermal cells.

In most roots, the stele is a vascular cylinder, a solid core of xylem and phloem (see Figure 35.13a). The xylem radiates from the center in two or more spokes, with phloem developing in the wedges between the spokes. In many monocot roots, the vascular tissue consists of a central core of parenchyma cells surrounded by alternating rings of xylem and phloem (see Figure 35.13b). The central region is often called pith but should not be confused with stem pith, which is ground tissue.

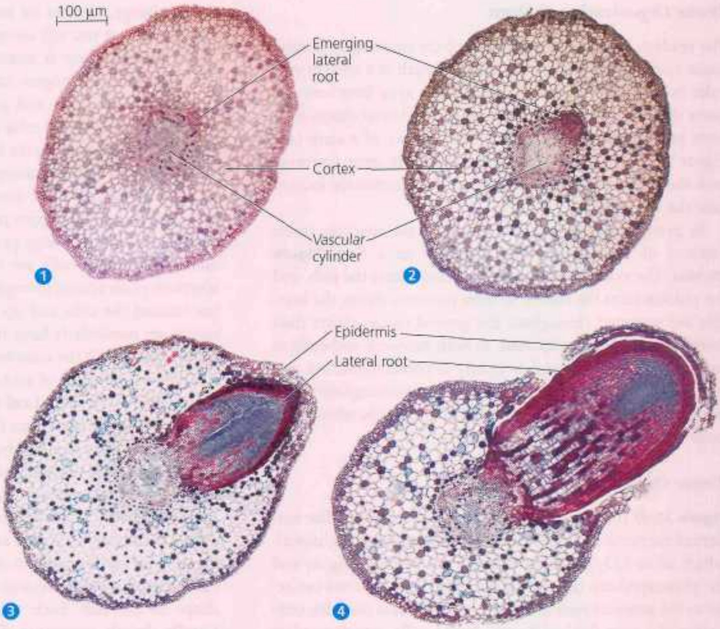
The ground tissue of roots, consisting mostly of parenchyma cells, fills the cortex, the region between the vascular cylinder



(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.

(b) Transverse section of a root with parenchyma in the center. The stele of many monocot roots is a vascular cylinder with a core of parenchyma surrounded by a ring of alternating xylem and phloem.

A **Figure 35.13 Organization of primary tissues in young roots.** Parts (a) and (b) show the three primary tissue systems in the roots of *Ranunculus* (buttercup) and *Zea* (maize), respectively. Note that the buttercup root has a central core of xylem and phloem, whereas the maize root has *a* core of parenchyma cells. These are two basic patterns of root organization, of which there are many variations, depending on the plant species. (All LMs)



▶ **Figure 35.14 The formation of a lateral root.** A lateral root originates in the pericycle, the outermost layer of the vascular cylinder of a root, and grows out through the cortex and epidermis. In this series of micrographs, the view of the original root is a transverse section, while the view of the lateral root is a longitudinal section.

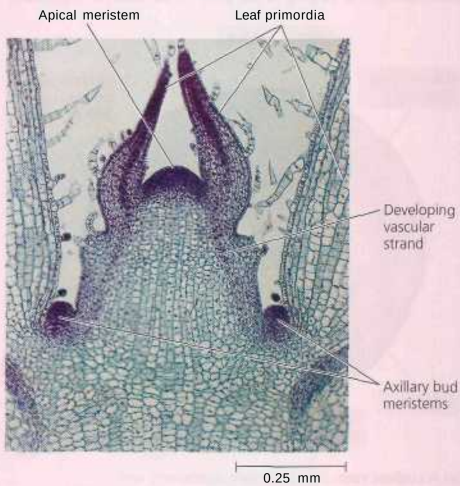
and epidermis. Cells within the ground tissue store organic nutrients, and their plasma membranes absorb minerals from the soil solution. The innermost layer of the cortex is called the endodermis, a cylinder one cell thick that forms the boundary with the vascular cylinder. You will learn in Chapter 36 how the endodermis is a selective barrier regulating passage of substances from the soil solution into the vascular cylinder.

Lateral roots arise from within the pericycle, the outermost cell layer in the vascular cylinder (see Figure 35.13). A lateral root elongates and pushes through the cortex and epidermis until it emerges from the established root **(Figure 35.14).** It cannot originate near the root's surface because it must remain connected with the vascular cylinder of the established root as part of the continuous vascular tissue system.

Primary Growth of Shoots

A shoot apical meristem is a dome-shaped mass of dividing cells at the tip of the terminal bud **(Figure 35.15).** Leaves arise as leaf primordia (singular, *primordium),* finger-like projections along the flanks of the apical meristem. Axillary buds develop from islands of meristematic cells left by the apical meristem at the bases of the leaf primordia. Axillary buds can form lateral shoots at some later time (see Figure 35.2).

Within a bud, leaf primordia are crowded close together because internodes are very short. Most of the actual elongation of the shoot occurs by the growth in length of slightly older internodes below the shoot apex. This growth is due to both cell division and cell elongation within the internode. Some plants, including grasses, elongate all along the shoot because there are meristematic regions called intercalary meristems at the base of each leaf. That is why grass continues to grow after being mowed.



▲ **Figure 35.15 The terminal bud and primary growth of a shoot.** Leaf primordia arise from the flanks of the apical dome. This is a longitudinal section of the shoot tip of *Coleus* (LM).

Tissue *Organization of* Stems

The epidermis covers stems as part of the continuous dermal tissue system. Vascular tissue runs the length of a stem in vascular bundles. Unlike lateral roots, which arise from vascular tissue deep within a root (see Figure 35.14), lateral shoots arise from preexisting axillary buds on the surface of a stem (see Figure 35.15). The vascular bundles of the stem converge with the roots vascular cylinder in a zone of transition located near the soil surface.

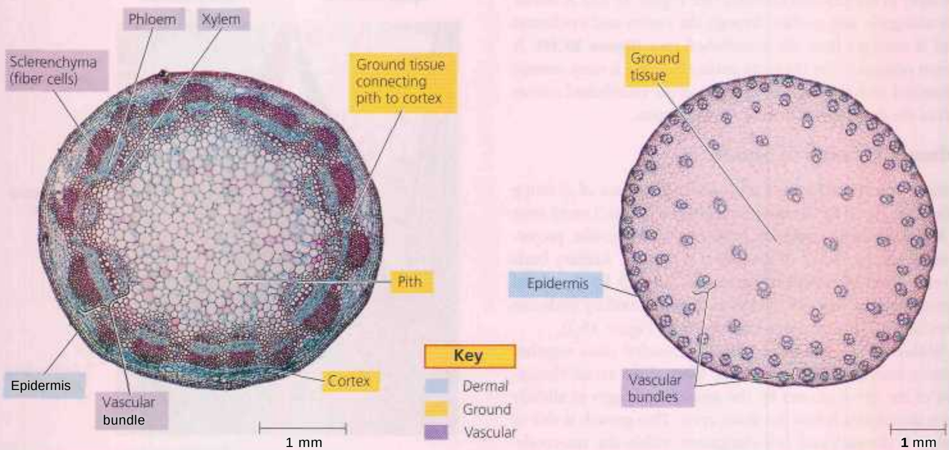
In gymnosperms and most eudicots, the vascular tissue consists of vascular bundles arranged in a ring **(Figure 35.16a).** The xylem in each vascular bundle faces the pith, and the phloem faces the cortex. In most monocot stems, the bundles are scattered throughout the ground tissue, rather than forming a ring **(Figure 35.16b).** In both monocot and eudicot stems, ground tissue consists mostly of parenchyma, but collenchyma cells just beneath the epidermis strengthen many stems. Sclerenchyma cells, specifically fiber cells within vascular bundles, also provide support.

Tissue *Organization of Leaves*

Figure 35,17 provides an overview of leaf structure. The epidermal barrier is interrupted by the stomata (singular, *sLoma),* which allow CO_2 exchange between the surrounding air and the photosynthetic cells inside the leaf. The term *stoma* can refer to the stomatal pore or to the entire stomatal complex consisting of a pore flanked by two guard cells, which regulate the opening and closing of the pore. In addition to regulating CO_2 exchange, stomata are major avenues for the evaporative loss of water, as you will see in Chapter 36.

The ground tissue is sandwiched between the upper and lower epidermis, a region called the **mesophyll** (from the Greek *mesos,* middle, and *phyll,* leaf). Mesophyll consists mainly of parenchyma cells specialized for photosynthesis. The leaves of many eudicots have two distinct areas: palisade mesophyll and spongy mesophyll. The palisade mesophyll, or palisade parenchyma, consists of one or more layers of elongated cells on the upper part of the leaf. The spongy mesophyll, also called spongy parenchyma, is below the palisade mesophyll. These cells are more loosely arranged, with a labyrinth of air spaces through which CO_2 and oxygen circulate around the cells and up to the palisade region. The air spaces are particularly large in the vicinity of stomata, where gas exchange with the outside air occurs.

The vascular tissue of each leaf is continuous with the vascular tissue of the stem. Leaf traces, connections from vascular bundles in the stem, pass through petioles and into leaves. Veins are the leaf's vascular bundles, which subdivide repeatedly and branch throughout the mesophyll. This network brings xylem and phloem into close contact with the photosynthetic tissue, which obtains water and minerals from the xylem and loads its sugars and other organic products into the phloem for shipment to other parts of the plant. The vascular structure also functions as a skeleton that reinforces the shape of the leaf. Each vein is enclosed by a protective bundle sheath, consisting of one or more cell layers, usually consisting of parenchyma.

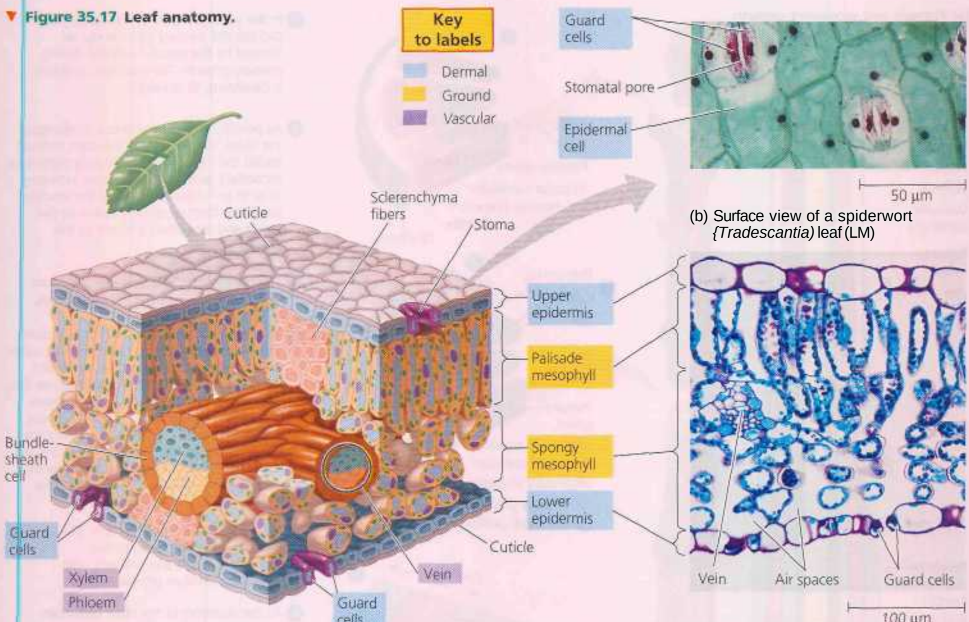


(a) A eudicot stem. A eudicot stern (sunflower), with vascular bundles forming a ring. Ground tissue toward the inside is called pith, and ground tissue toward the outside is called cortex. (LM of transverse section)

(b) A monocot stem. A monocot stem (maize) with vascular bundles scattered throughout the ground tissue. In such an arrangement, ground tissue is not partitioned into pith and cortex. (LM of transverse section)

***A* Figure 35.16 Organization of primary tissues in young stems.**

▼ Figure 35.17 Leaf anatomy.



(a) Cutaway drawing of leaf tissues

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

(c) Transverse section of a lilac (Syringa) leaf (LM)

Concept Check 35.3

1. Describe how roots and shoots differ in their branching.
2. Contrast primary growth in roots and shoots.
j 3. Describe the functions ol leaf veins.

For suggested answers, see Appendix A,

Concept 35.4

J Secondary growth adds girth to sterns and roots in woody plants

Secondary growth, the growth in thickness produced by lateral meristems, occurs in stems and roots of woody plants, but rarely in leaves. The secondary plant body consists of the tissues produced by the vascular cambium and cork cambium. The vascular cambium adds secondary xylem (wood) and secondary phloem. Cork cambium produces a Lough, thick covering consisting mainly of cork cells.

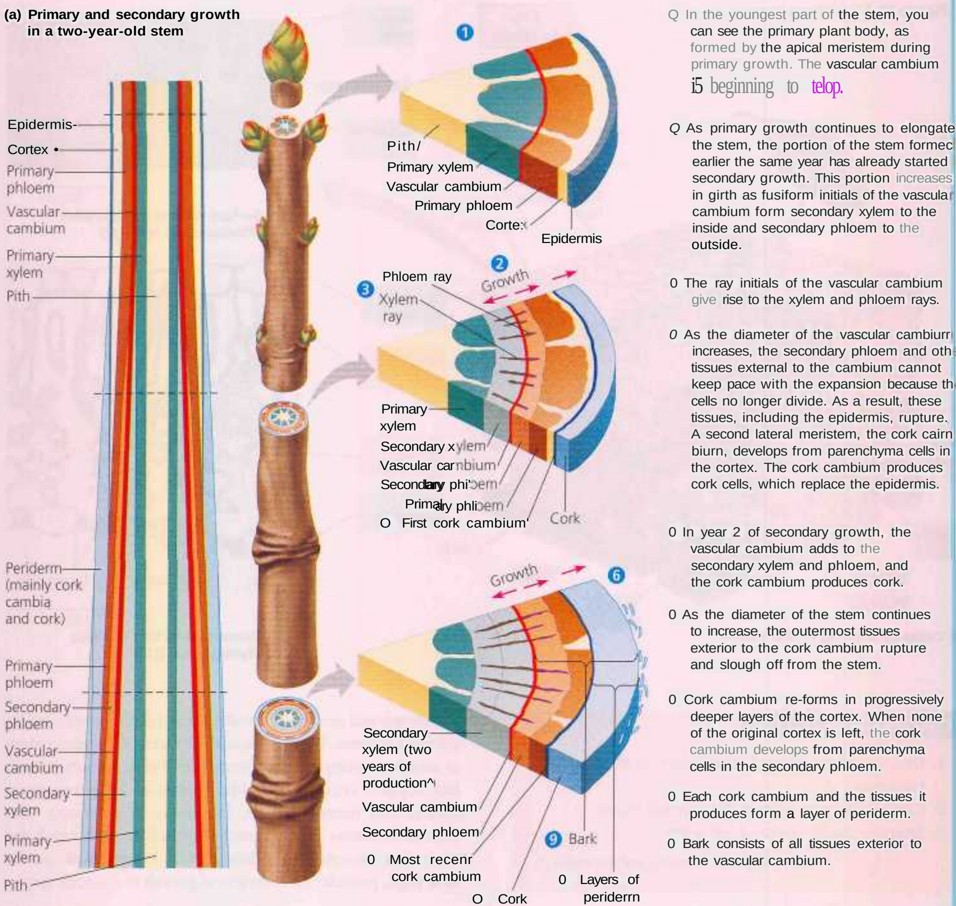
Primary and secondary growth occur simultaneously but in different regions. While an apical meristem elongates a stem or root, secondary growth commences where primary growth has stopped, occurring in older regions of all gymnosperm species and many eudicots, but rarely in monocots. The process is similar in stems and roots, which look much the same after extensive secondary growth. **Figure 35.18,** on the next page, provides an overview of growth in a woody stem.

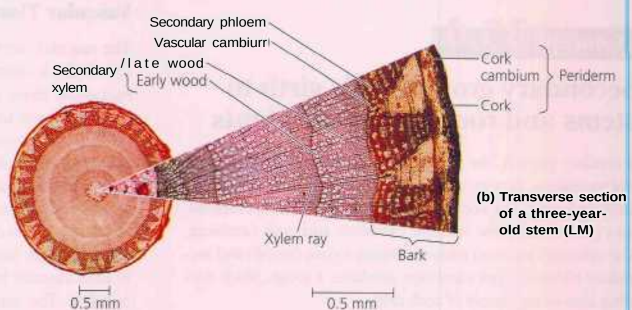
The Vascular Cambium and Secondary Vascular Tissue

The vascular cambium is a cylinder of meristematic cells one cell thick. It increases in circumference and also lays down successive layers of secondary xylem to its interior and secondary phloem to its exterior, each layer with a larger diameter than the previous layer (see Figure 35.18). In this way, it is primarily responsible for the thickening of a root or stem.

The vascular cambium develops from undifferentiated cells and parenchyma cells that regain the capacity to divide. In a typical gymnosperm or woody eudicot stem, the vascular cambium forms in a layer between the primary xylem and primary phloem of each vascular bundle and in the ground tissue between the bundles. The meristematic bands within and between the

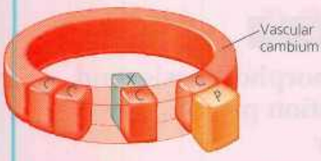
(a) Primary and secondary growth in a two-year-old stem



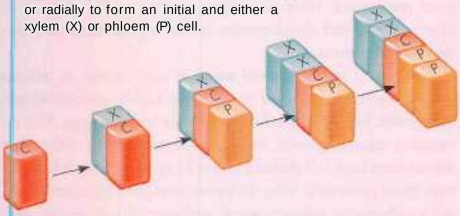


(b) Transverse section of a three-year-old stem (LM)

▲ Figure 35.18 Primary and secondary growth of a stem. You can track the progress of secondary growth by examining the sections through sequentially older parts of the stem. (You would observe the same changes if you could follow the youngest region, near the apex, for the next three years.)



(a) Types of cell division. An initial can divide transversely to form two cambial initials (C) or radially to form an initial and either a xylem (X) or phloem (P) cell.



(b) Accumulation of secondary growth. Although shown here as alternately adding xylem and phloem, a cambial initial usually produces much more xylem.

▲ **Figure 35.19 Cell division in the vascular cambium.**

vascular bundles unite to become a continuous cylinder of dividing cells. In a typical gymnosperm or woody eudicot root, the vascular cambium forms in segments between the primary phloem, the lobes of primary xylem, and the pericycle, eventually becoming a cylinder.

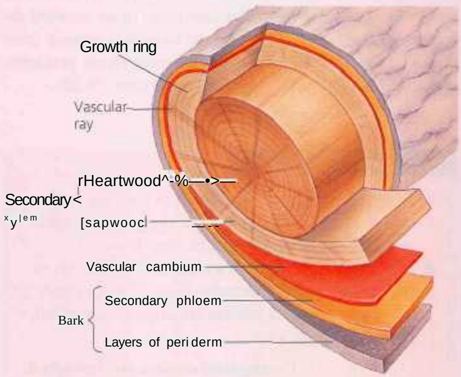
Viewed in transverse section, the vascular cambium appears as a ring, with interspersed regions of cells called fusiform initials and ray initials. When these initials divide, they increase the circumference of the cambium itself and add secondary xylem to the inside of the cambium and secondary phloem to the outside **(Figure 35.19).** Fusiform initials produce elongated cells such as the tracheids, vessel elements, and fibers of the xylem, as well as the sieve-tube members, companion cells, parenchyma, and fibers of the phloem. They have tapered (fusiform) ends and are oriented parallel to the axis of a stem or root. Ray initials, which are shorter and oriented perpendicular to the stem or root axis, produce vascular rays—radial files consisting mainly of parenchyma cells. Vascular rays are living avenues that move water and nutrients between the secondary xylem and secondary phloem. They also store starch and other organic nutrients. The portion of a vascular ray located in the secondary xylem is known as a xylem ray The portion located in the secondary phloem is called a phloem ray.

As secondary growth continues over the years, layers of secondary xylem (wood) accumulate, consisting mainly of tracheids, vessel elements, and fibers (see Figure 35.9). Gymnosperms have tracheids, whereas angiosperms have both tracheids and vessel elements. Dead at functional maturity, both types of cells have thick, lignified walls that give wood its hardness and strength. Tracheids and vessel elements that develop early in the growing season, typically in early spring, are known as early wood and usually have relatively large diameters and thin cell walls (see Figure 35.18b). This structure maximizes delivery of water to new, expanding leaves. Tracheids and vessel elements produced later in the growing season, during late summer or early fall, are known as late wood. They are thick-walled cells that do not transport as much water but do add more support than do the thinner-walled cells of early wood.

In temperate regions, secondary growth in perennial plants is interrupted each year when the vascular cambium becomes dormant during winter. When growth resumes the next spring, the boundary between the large cells of the new early wood and the smaller cells of the late wood produced during the previous growing season is usually a distinct ring in the transverse sections of most tree trunks and roots. Therefore, a tree's age can be estimated by counting its annual rings. The rings can have varying thicknesses, reflecting the amount of seasonal growth.

As a tree or woody shrub ages, the older layers of secondary xylem no longer transport water and minerals (xylem sap). These layers are called heartwood because they are closer to the center of a stem or root **(Figure 35.20).** The outer layers still transport xylem sap and are therefore known as sapwood. That is why a large tree can still survive even if the center of its trunk is hollow. Because each new layer of secondary xylem has a larger circumference, secondary growth enables the xylem to transport more sap each year, supplying an increasing number of leaves. Heartwood is generally darker than sapwood because of resins and other compounds that clog the cell cavities and help protect the core of the tree from fungi and wood-boring insects.

Only the youngest secondary phloem, closest to the vascular cambium, functions in sugar transport. As a stem or root increases in circumference, the older secondary phloem is sloughed off, which is why secondary phloem does not accumulate as extensively as does secondary xylem.



▲ **Figure 35.20 Anatomy of a tree trunk.**