Chapter 7

The Root System

KEY CONCEPTS

1. The principal functions of roots are absorption of water and nutrients, conduction of absorbed materials into the plant body, and anchorage of the plant in the soil. Many roots have relationships with bacteria and fungi in the rhizosphere (soil zone near the root).

2 . The root is initiated in the embryo as the radicle. It penetrates into the soil and forms branches.

3 . The root tip is composed of the root cap, the root apical meristem, the region of cell elongation, and the region of cell maturation.

4 . Roots are composed of the following tissues: epidermis, cortex, endodermis, pericycle, xylem, and phloem.

5. The endodermis regulates ion movement into the xylem. The Casparian strip embedded in the cell wall inhibits mineral movement through the wall. The pericycle is the site of lateral root initiation and contributes to vascular cambium and cork cambium formation.

7.1 THE FUNCTIONS OF ROOTS

Although plant biologists have studied plants for hundreds of years, they have largely ignored the root system and its functions. This is probably because roots are underground, where they cannot be seen. Though they are hidden from view, roots play a critical role in the everyday activities of plants. The main functions of roots are anchorage of the plant body in the soil (or to a surface, in the case of some vines); absorption of water and minerals from the soil; storage of foods; and conduction of food and water from the soil and from storage reserves into the shoot. Other root functions are also described in this chapter.

The root system becomes more complex as the plant grows from a single root in a young seedling to a massive system of branched roots, often weighing tons in large trees. During all stages in a plant's growth cycle, there is a balance between the shoot system and the root system (Fig. 7.1). The root system must be able to supply the shoot with sufficient water and mineral nutrients, and the shoot system must manufacture enough food to maintain the root system.

The contact zone between the root surface and the soil is called the rhizosphere (Fig. 7.2). This region, only a few millimeters thick, is a very interesting and unique zone. Its complex chemistry includes organic material, gases, and nutrients from the roots. Consequently, the bacteria and fungi near roots are often richer and more diverse than in soil farther away. Soil fungi and bacteria form important symbiotic (mutually beneficial) relationships with roots. These will also be discussed later in the chapter.

Every time you try to pull weeds you are reminded of the *anchorage* function of roots. Plants with unusual roots provide anchorage in atypical ways. In ivy *(Hedera helix)* and the climbing fig *(Ficus pumila;* see sidebar: *The Climbing Fig And Its Adhesive Pads)* clusters of roots develop from the stems to form an unusual adhesive pad allowing

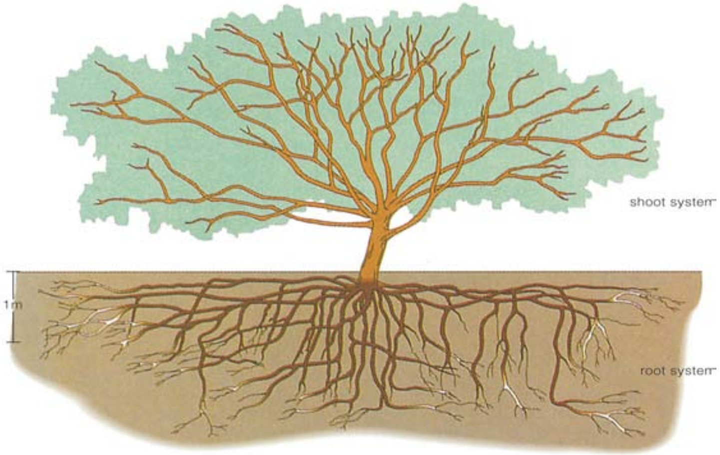


Figure 7.1. Root and shoot systems of a tree at least 10 years old. Note that the majority of the roots lie within the upper 1 m of soil and that the total volume of roots is equal to or greater than the shoot branches.

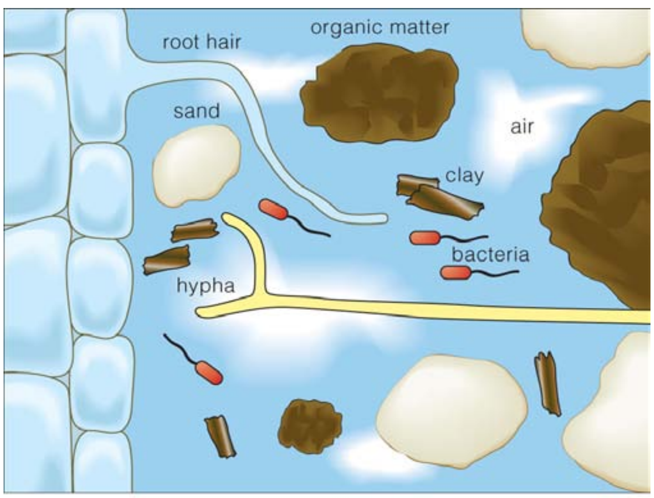


Figure 7.2. The soil area immediately around a root is called the rhizosphere. This area, shown near the root tip, is rich in soil microorganisms, bacteria and fungi, and in nutrients from the root body and from sloughed-off root cap cells.

these vines to cling to vertical surfaces. Parasitic plants like dodder (*Cuscuta* sp.) sink specialized roots into their host and then tap into its water and nutrient supply.

All plants need water. In herbaceous (non-woody) plants, water accounts for about 90% of the plant's weight. Water is needed for all root processes and for every metabolic reaction. Plants also need the dissolved salts and minerals, such as potassium, sulfur, phosphorus, calcium, and magnesium, contained in the soil water. For these reasons, plants have developed an elaborate system in roots for the *absorption* and *conduction* of water.

All roots, even slender ones with a primary function of absorption, may temporarily store small amounts of food. For example, when sugar moves into roots more rapidly than can be used by growing cells, it may be converted to starch and stored. During slow growth periods, rather large quantities of starch are stored in woody roots of orchard trees. This food constitutes a reserve that is used when flowering and active growth are resumed in spring. Carrots (*Dacus carota*), and beets (*Beta vulgarus*) are common root crops.

7.2 TYPES OF ROOT SYSTEMS

There are two basic types of root systems: fibrous and tap. They are distinguished by the way they develop and by their appearance. Many grasses and small garden plants, for instance, when pulled up bring with them a massive clump of soil. This happens because the **fibrous root system** of these plants consists of several main roots that branch to form a dense mass (Fig. 7.3a, b). A typical annual grass such as corn (*Zea mays*) or rye (*Elymus cereale*) will build an immense fibrous root system in one growing season. A single rye plant 50 cm (20 in) tall, with 80 tillers (shoot branches), may have a root system surface area of about 210 m^2 (1890 ft^2), compared to only about 5 m^2 (45 ft^2) for its aboveground shoot system.

Plants with a large storage root, like carrot (*Daucus carota*), have a **tap root system**, consisting of one main root from which lateral roots branch (Fig. 7.3c). Some desert plants have a rapidly growing tap root system that enables them to penetrate the soil quickly to reach deep sources of water.

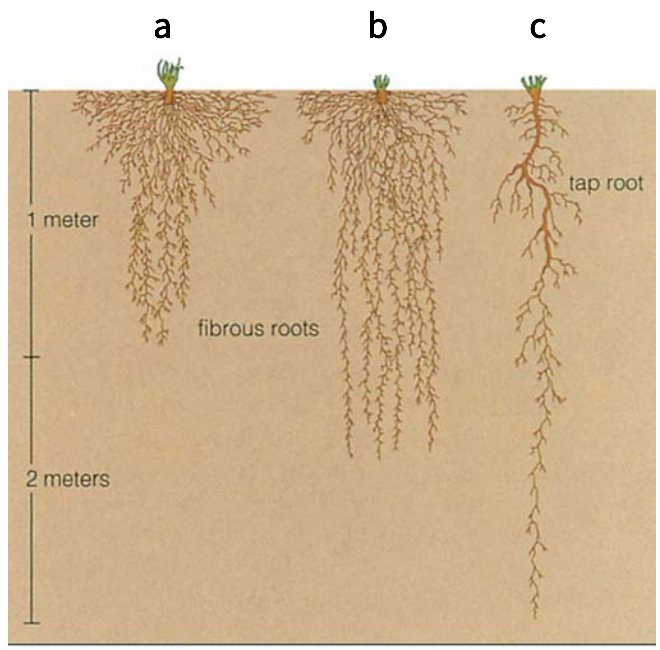


Figure 7.3. Fibrous and tap root systems. (a) Shallow, spreading, fibrous root system. (b) Fibrous root system penetrating the soil evenly up to 1 meter in this example. (c) Tap root system, in which main primary root penetrates soil 2 meters or more.

Differences in the Design of Root Systems Help Plants Compete for Water and Minerals

Plants that grow in close proximity compete for water, mineral nutrients, and light energy. As will be discussed in Chapter 26, plants reduce the effects of competition by utilizing different parts of the environment, including the soil. This is one reason why root systems of different species also occupy different depths in the soil.

When plants growing in the prairie in the middle United States are carefully excavated, three general categories of roots are evident, based on how deep the roots grow (Fig. 7.3). Some grassland species, such as blue grama *(Bouteloua gracilis)*, possess a very shallow root system, most of the roots being within the top 15 cm (6 in) of soil. Other species, such as buffalo grass *(Buchloe dactyloides)*, have evenly distributed roots as deep as 1.5 m (60 in). Still others, such as locoweed *(Crotalaria sagittalis)*, have a tap root system, which lacks width but runs deep. By using different depths of the soil, these plants reduce competition for moisture and dissolved minerals.

Plants Have Different Types of Roots

When seeds germinate, the embryonic root (the **radicle**--see Chapter 14) extends by the division and elongation of cells to form the primary root (Fig. 7.4a). Tap root systems develop from one primary root, which then forms lateral roots. Further branching results in successive orders of roots. Fibrous root systems develop in a slightly different way. The embryos of most grasses have a single radicle, but in addition several other embryonic roots form just above the radicle; these are called **seminal roots**. The seminal roots emerge soon after the radicle, and all of these roots branch, making a fibrous root system (Fig. 7.4b).

Roots called **adventitious roots** originate on leaves and stems. There are several common examples of adventitious roots. In a young corn plant, soon after germination

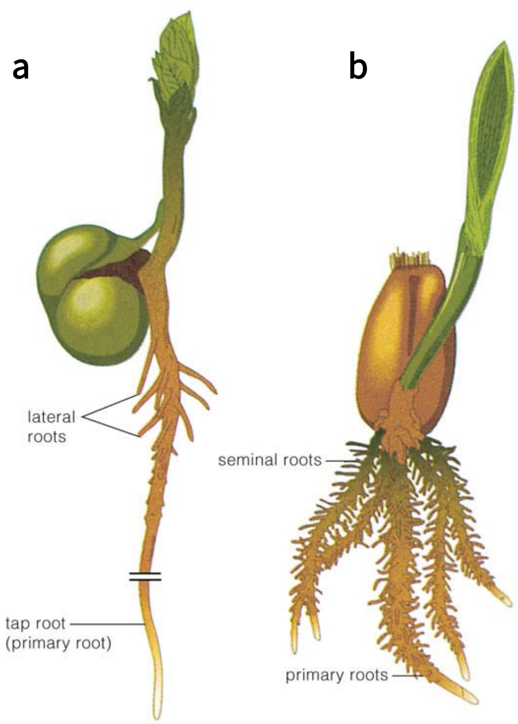


Figure 7.4. (a) Seedling of pea (*Pisum sativum*) with a tap root and several lateral roots. (b) Seedling of wheat (*Triticum aestivum*). Seminal roots emerge from the hypocotyl (these are adventitious roots since they do not emerge from another root) and create the fibrous root system.

prop roots develop on the stem just above the soil (Fig. 7.5a). Prop roots absorb water and minerals, but they also support the plant in the soil.

Banyan *(Ficus bengalensis)* trees grow in the salty mud of tropical lagoons and tidal marshes. Branches of these trees form adventitious roots--also called aerial roots, because they are exposed to air. These extend down from branches into the soil, where they enlarge and actually hold up the large branches (Fig. 7.5b). These roots absorb water and nutrients, but their most important function is to prop up the stem. In India, merchants once held open-air bazaars among the prop roots and expansive branches of the banyan.

Mangrove trees *(Rhizophora* mangle*)* are native to low tidal shores and marshes in tropical and subtropical regions. In the mangrove (Fig. 7.5c) small adventitious roots called

pneumatophores, stick up from the mud. These roots absorb oxygen and increase its availability to the submerged roots. There are many other examples of adventitious roots.

Pieces of stem, such as a cane from a blackberry plant or a branch of willow, can be induced to make roots from their cut ends simply by placing them in moist soil. Leaves from *Begonia* and several other plants also can be rooted, simply by soaking them in water. Many commercially important ornamentals are reproduced by root propagation from the leaves or stems.

7.3 THE DEVELOPMENT OF ROOTS

The tips of functional roots are thin (Fig. 7.4a) and usually white. If you were to dig up the roots of a big tree, you would see many very large roots, each of which could be followed through its branches to a thin, white tip. These tiny root tips are important parts of the root system because it is here, in just a few millimeters, where many of the important functions of roots take place.

Figure 7.5. Types of adventitious roots. (a) Corn (*Zea mays*) stem showing prop roots, which emerge from the stem just above the soil. These roots help support the shoot system. (b) Extensive adventitious root system of mangrove (*Rizophora mangle*) growing in the tidal zone of Australia's tropical coast. Note the many air roots (pneumatophores) sticking into the mud. (c) Banyan (*Ficus bengalensis*) tree with an extensive aerial root system.

The Root Tip Is Organized into Regions and Protected by a Root Cap

In a longitudinal section of a root tip viewed through a microscope, it is apparent that the cells are organized into three regions: the **root apical meristem**, the **region of elongation**, and the **region of maturation** (Fig. 7.6a). The developmental events that take place in the cells of each region are somewhat specific, but the regions do overlap (Fig. 7.6b).

The root cap at the tip of the root apex protects the root apical meristem (RAM), a group of small, regularly shaped cells, most of which are dividing. These cells are organized into two different patterns (Figure 7.7a, b). A small, centrally located part of the RAM is called the quiescent center (QC) (Fig. 7.8) because its cells divide at an extremely slow rate. The function of the QC is not exactly known, but it seems to be activated during times of acute stress. It may be a site for the synthesis of plant hormones important for controlling root development.

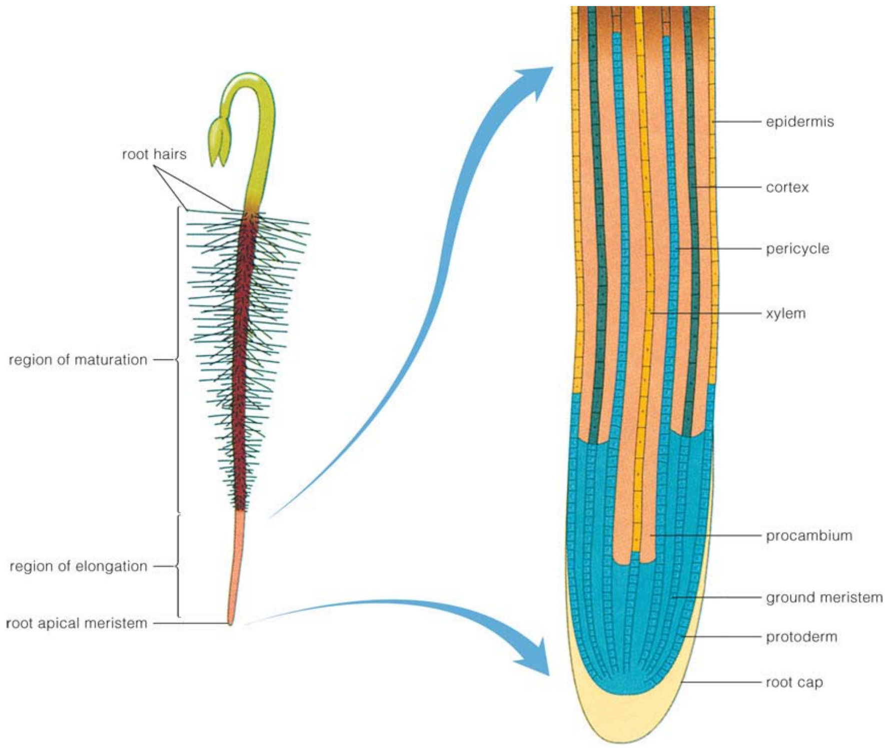


Figure 7.6. Regions of the root tip. (left) Radish seedling (*Raphanus sativus*) showing the root apical meristem, region of elongation, and region of maturation containing root hairs. (right) Median longitudinal section of root tip. Procambium cells tend to stop dividing before ground meristem cells, protoderm and pericycle cells continue divided farther back in the root. All cells stop elongating at approximately the same point. Primary tissue cell maturation also may occur at different positions.

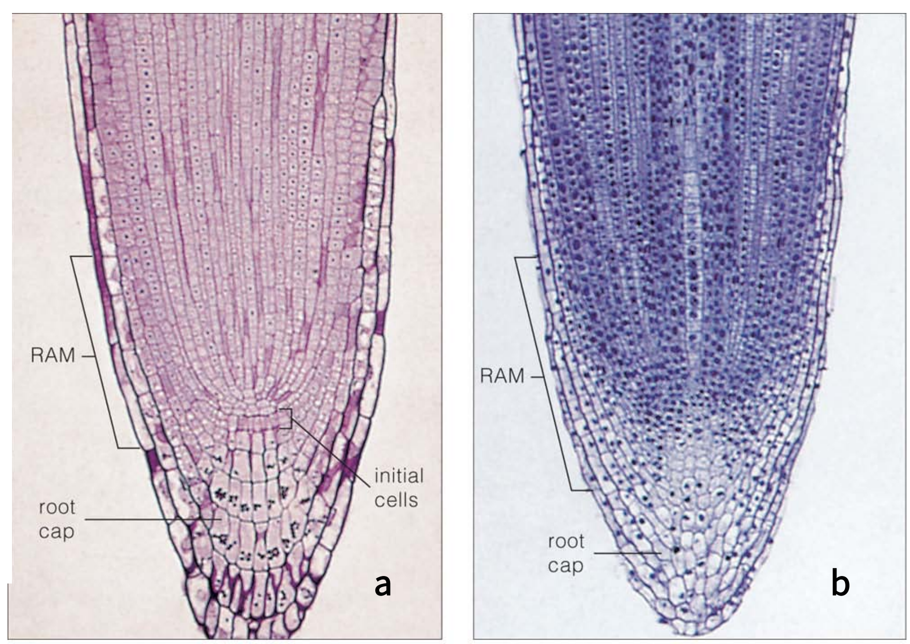
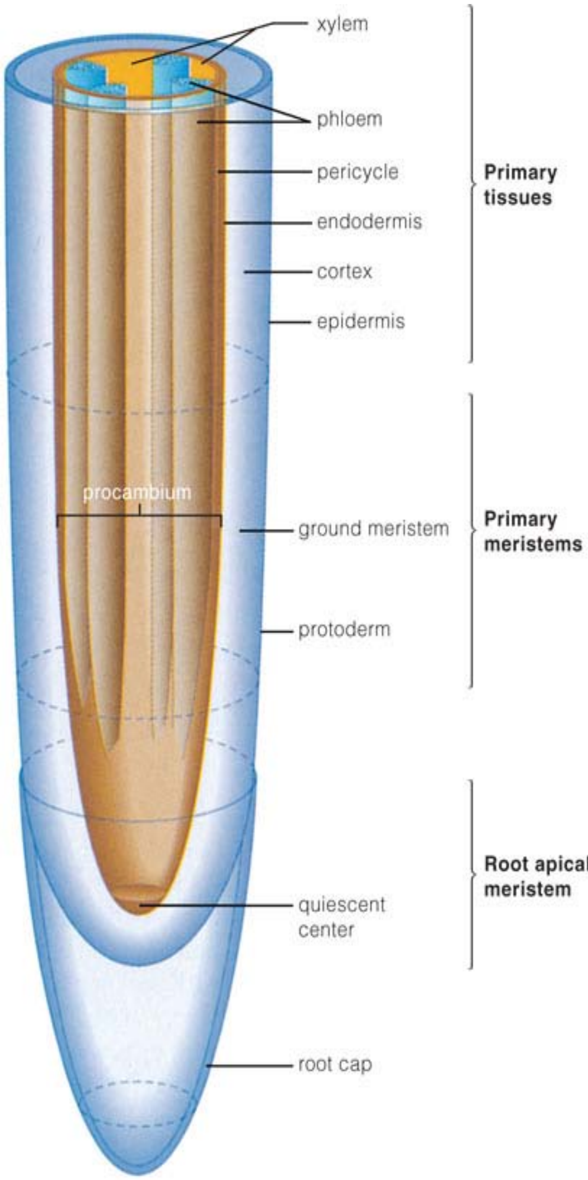


Figure 7.7. The patterns of RAM divisions. (a) Longitudinal section of the root tip of flax (*Linum grandiflorum*). Notice that all cell files connect directly to specific tiers of cells just above the root cap. X200. (b) Longitudinal section of onion (*Allium cepa*) root tip. In this type of root apex the cell files terminate at a group of cells without any apparent organization. X81.



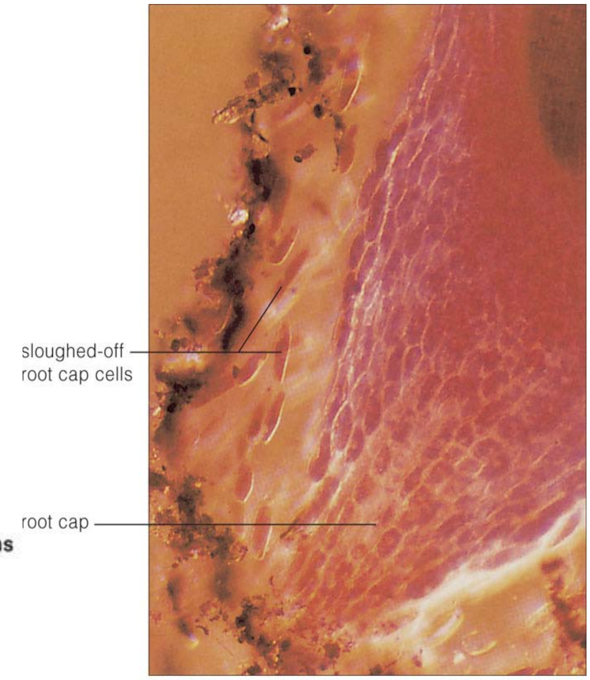


Figure 7.9. (above) Corn (*Zea mays*) root cap with sloughed root cap cells in the soil, X60.

Figure 7.8. (left) Three-dimensional diagram of a root in longitudinal view to show the relative positions of the primary meristems and primary tissues. The quiescent center is a small group of cells that are metabolically quiescent.

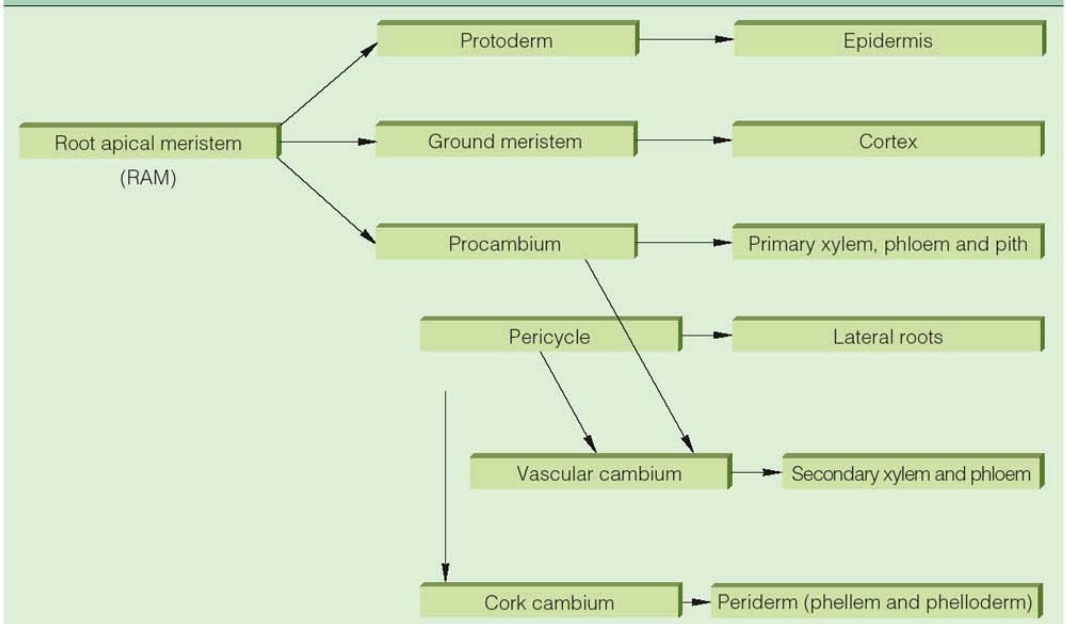
Cells just apical to the QC divide and produce cells to form the root cap (Fig. 7.7, 7.8), the thimble-shaped layer of cells that protect the RAM as the root elongates and pushes through the soil. The root cap is also the site of gravity perception, which controls the direction of root growth . Root cap cells are constantly being sloughed off at the very tip, but new cells are added by the apical meristem. The sloughed-off cells can remain alive in the soil for a time, where they provide nutrients for soil bacteria and fungi in the rhizosphere (Figs. 7.2, 7.9).

Just basal to the meristem region, toward the body of the root, is the region of elongation. Careful examination of a longitudinal section of a root shows that the boundary where cells stop dividing and start elongating is different for each tissue (see Fig. 7.6b). The region of maturation is the site of root hair formation and the maturation of other cell types. The precise position of cell maturation in different cell files is variable; cells in some files mature close to the tip, and others mature farther back (Fig. 7.6b).

The RAM Forms Three Primary Meristems

As mentioned in Chapter 4, cells change their structure according to their position, and in roots the process of change begins in the root apical meristem. The RAM differentiates into three primary meristems: the **protoderm**, **ground meristem**, and **procambium** (see Fig. 7.8). These then go on to become the primary tissues of the root, as described in the following pages and as summarized in Table 7.1.

Table 7.1 Summary of Tissues and Meristems in Roots



7.4 THE STRUCTURE OF ROOTS

The Epidermis, Cortex, and Vascular Cylinder Are Composed of Specialized Tissues

EPIDERMIS Protoderm cells differentiate into the epidermis, which in roots is composed mostly of long epidermal cells. Some cells of the protoderm develop into **root hairs** (Fig. 7.10) by the extension of epidermal cell walls into the surrounding soil. Root hairs may be quite long, but they are only one cell. The cell walls of root hairs are thin and composed principally of cellulose and pectic substances. Root hairs tend to be sticky, so that soil particles cling to them (Fig. 7.10b). In most plants, the life of any one root hair is short; it functions for only a few days or weeks. New hairs are constantly forming at the apical end of the roothair zone, while those at the basal end are dying. Thus, as the root advances through the soil, fresh, actively growing root hairs are constantly coming into contact with new soil particles. In the rye plant, root hairs develop at an average rate in excess of 100 million per day.

Root hairs account for a major fraction of the surface area of the root tip, and thus they generally play a major role in the absorption of water and nutrients from the soil. Although nearly all ordinary land plants possess root hairs, a few plants, such as some gymnosperm trees, like firs, apparently lack them. Also, many aquatic plants have no root hairs. Moreover, land plants (corn, for example) that normally develop root hairs when the root system grows in the soil may develop no root hairs when the roots grow in water. In plants devoid of root hairs, absorption is accomplished entirely through the epidermal cells.

The epidermis in roots is usually one cell layer thick; but in the aerial roots of certain plants, such as orchids, a multilayered epidermis develops that stores and possibly absorbs water from the moist air.

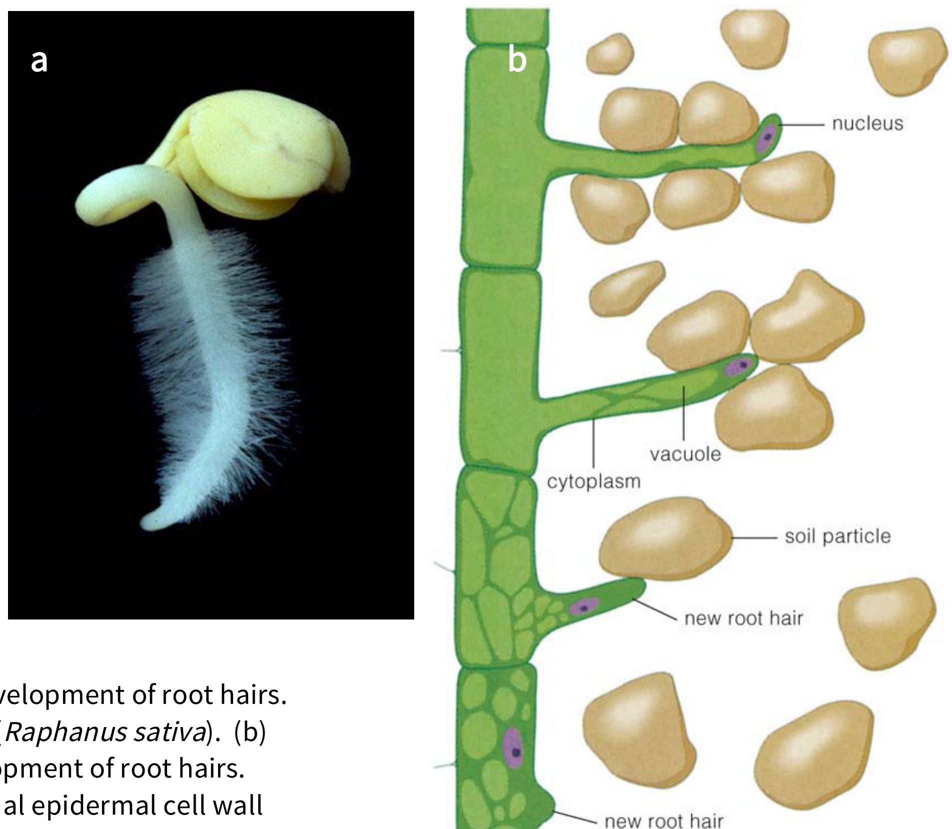
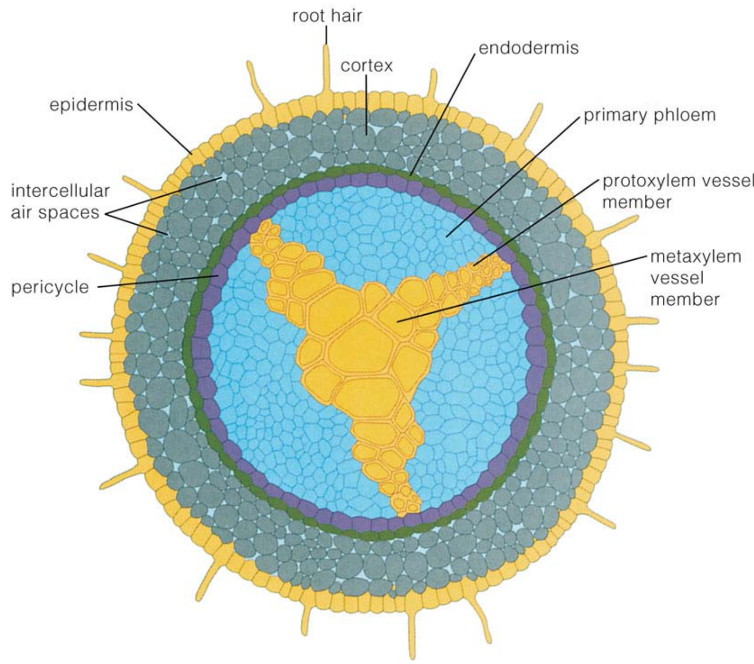


Figure 7.10. The development of root hairs. (a) Radish seedling (*Raphanus sativa*). (b) Stages in the development of root hairs. Note that the external epidermal cell wall protrudes and that the cell cytoplasm and nucleus move into the root hair near the tip. Root hairs are in close contact with soil particles and increase the water absorptive surface of the root.

Figure 7.11. (a) A dicot root cross section from the area where maximum absorption occurs. The epidermis contains root hairs. The cortex has abundant air spaces between parenchyma cells. The endodermis is bounded by a Casparian strip. The pericycle is one cell-layer thick. The primary xylem is distributed into three protoxylem points, with metaxylem in the middle of the root. The primary phloem alternates with primary xylem. Residual procambium not shown) occurs between the primary xylem and primary phloem.



CORTEX The root cortex is derived from ground meristem and is composed chiefly of parenchyma cells. The innermost layer of the cortex, a single row of cells called the **endodermis** (Figs. 7.11, 7.12a, b) plays a special role in controlling mineral accumulation by the root. This is the role of the **Casparian strip**, a waxy material embedded in the upper, lower (transverse), and side (radial) walls of endodermal cells (Fig. 7.12).

Water and dissolved minerals from the soil can move from cell to cell by two paths; they can travel through the porous walls of the cortex and epidermis, or they can move through the living cells (Fig. 7.12c, d). Movement through the cell wall is free movement without any constraints. Movement into a living cell, however, is regulated because it involves crossing the plasma membrane. Some substances can move across the membrane by diffusion. Some minerals, for example potassium, can be moved across membranes through special proteins ("channels") embedded in the membrane. Some proteins can actually pump minerals into a living cell, even against a diffusion gradient.

The function of the endodermis is to guarantee that the minerals that finally reach the vascular cylinder can do so only by first passing across at least one plasma membrane. One reason this is important in roots is that it provides a mechanism to increase the concentration of needed minerals through pumps in the endodermis cell membrane.

In roots of many plants, an **exodermis** containing Casparian strips occurs at the outer layer of the cortex, just inside the epidermis. This layer is present in many grass roots and in the aerial roots of orchids (Fig. 7.13). The exodermis apparently also functions to regulate ion absorption and accumulation.

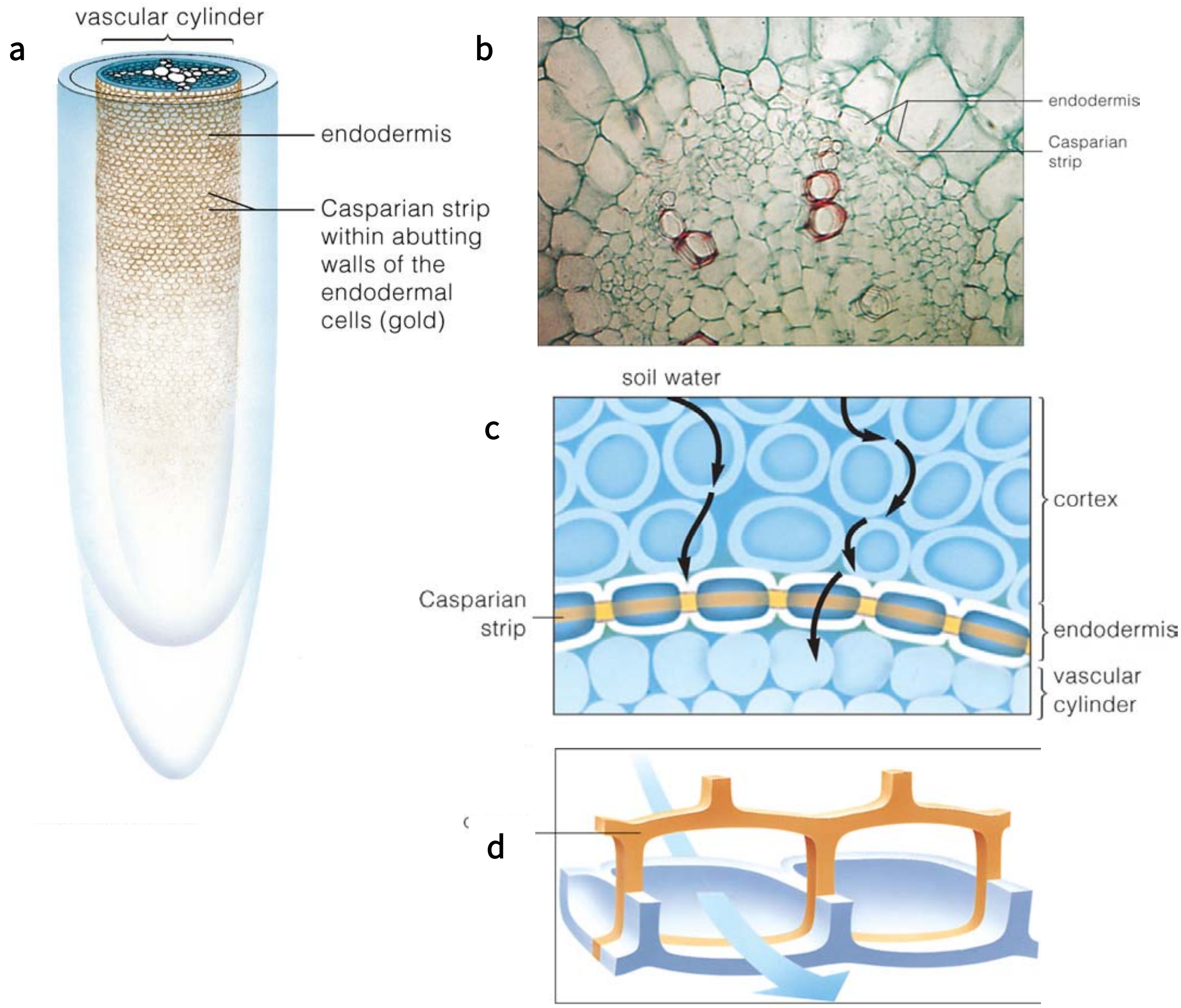


Figure 7.12. Control of nutrient movement into the xylem is a function of the endodermis. (a, b) The endodermis is a single layer of inner cortex cells which have a waxy strip (Casparian strip) embedded into their transverse and radial cell walls. (c) The strip keeps water from moving indiscriminately through the cell walls and into the vascular cylinder. (d) The Casparian strip makes water move through the endodermal cells and in this way the plasma membrane can selectively control the uptake of nutrients.

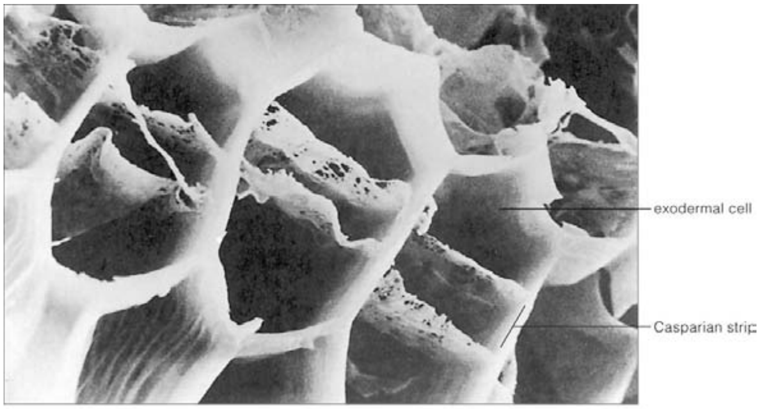


Figure 7.13. The Casparian strip in exodermis cells of an aerial root of *Epidendrum* orchid. The plasma membrane has been pulled away from the cell wall by soaking the roots in salt solution. This SEM shows that the membrane is attached at the Casparian strips. X800.

VASCULAR CYLINDER The entire central cylinder of roots is composed of vascular tissue that differentiates from the procambium cells (Fig. 7.14). In roots of dicot plants the primary xylem usually consists of a central core of xylem elements organized into two or more radiating points (Fig. 7.11a). In most monocot roots the very center of the root is composed of parenchyma cells with the primary xylem and phloem forming in a ring (Fig. 7.11b). The first xylem elements to mature, the protoxylem, develop at the outer points of the xylem (Figs. 7.11, 7.14b). Metaxylem, the last primary xylem to mature, differentiates in the center of the vascular cylinder (Fig. 7.14b, c).

The protoxylem is capable of transporting water while the root is elongating, which requires both the strength to withstand the forces that move water and still be flexible enough to stretch as the root elongates. This dual ability comes from a secondary cell wall in the shape of annular rings or spirals (see Fig. 4.9).

Metaxylem cells mature in regions of the root where elongation has been completed. Because they are no longer required to elongate, they form thick secondary cell walls with pits through which lateral exchange of water and minerals may take place. Protoxylem cells often become crushed after the metaxylem develops, but by then these cells are not needed.

In roots of monocots like asparagus (*Asparagus officinale*), a central region of parenchyma cells forms (Fig. 7.15). This region is sometimes called a pith, which refers to the location of ground tissue in the center of stems, which is formed from ground meristems. However, in roots it is part of the vascular cylinder and originates from procambium. Xylem (both protoxylem and metaxylem) of roots consists of several other cell types, including vessel elements, tracheids, parenchyma, and fibers.

Phloem cells form in the areas between the protoxylem arms (Figs. 7.11, 7.14). The protophloem is actually the first part of the vascular system to become functional. These cells form at the periphery of the phloem and function primarily during root elongation. Metaphloem develops toward the inside and functions during the plant's adult life. Phloem of roots may consist of parenchyma, fibers, sieve-tube members, and companion cells.

The outer boundary of the vascular cylinder is the **pericycle** (Figs. 7.11, 7.14c). This tissue is unique, in that it remains capable of dividing for a long time. It has three functions in dicot roots: (1) It is the site where the development of lateral roots is initiated, (2) it contributes to the formation of vascular cambium, and (3) it contributes to the formation of the cork cambium. In monocot roots no secondary growth occurs, so pericycle is involved only in lateral root initiation. The pericycle is usually one cell layer thick, but in some roots it has multiple layers.

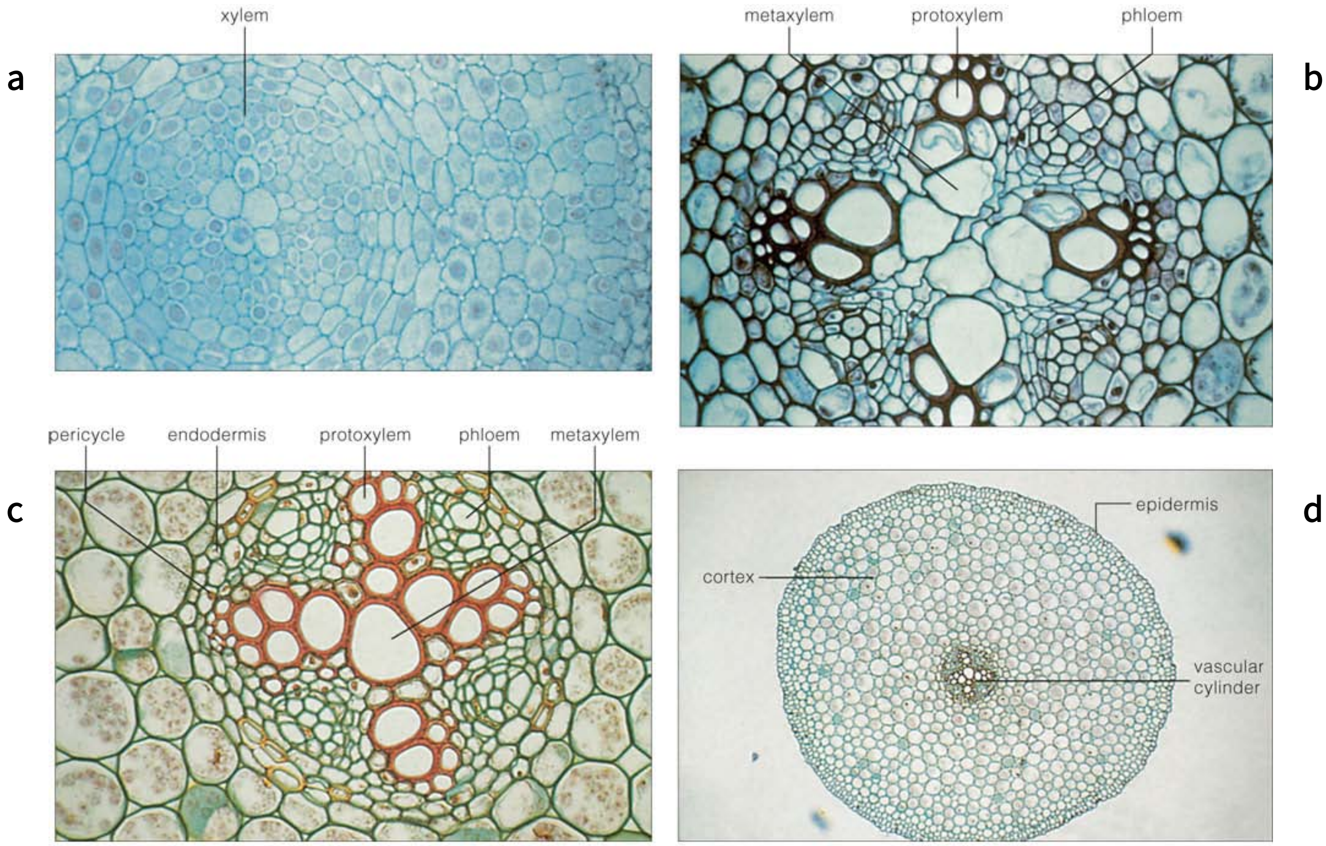


Figure 7.14. Differentiation in the primary growth of buttercup (*Ranunculus* sp.) roots. (a) Immature region, where no secondary walls have yet formed in the xylem. X170. (b) The cells of the protoxylem have developed secondary walls (shown here stained red with safranin). This particular root has four protoxylem points with phloem between. X190. (c) Fully mature root with all primary tissues differentiated. Note that the endodermal cells adjacent to the protoxylem points are lacking secondary walls. X170. (d) The same section as (c), but showing all tissues. X190.

Lateral Roots are Initiated in the Pericycle

The initiation of lateral roots at particular locations is controlled by chemical growth regulators that cause pericycle cells to begin dividing at specific sites (Fig. 7.16a). The **lateral root primordia** that result (Fig. 7.16d) continue to form new cells, which in turn elongate. Endodermal cells outside the primordium also divide for a short time, contributing cells to the tip of the new lateral root. As it expands (Fig. 7.16b), the lateral root pushes its way through and destroys the cortical cells and the outer epidermis. The breakdown of these cortical cells is thought to be at least partly the result of digestive enzymes released from the lateral root primordium. As the lateral root emerges, its cells become organized into a root cap and root apical meristem (Fig. 7.16c, d). The wound formed by lateral root emergence is quickly healed by the secretion of mucilage and waxy substances by adjacent cortical cells. The vascular system of the main root axis and the lateral roots is connected (Fig. 7.16e).

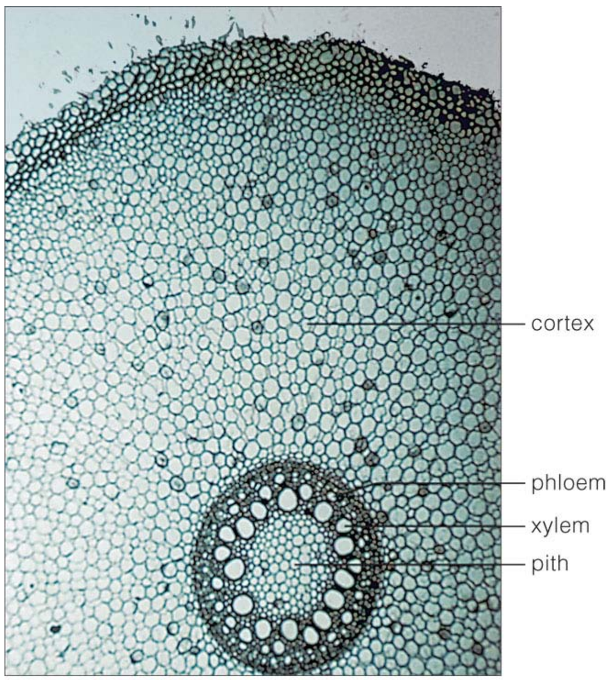


Figure 7.15. *Asparagus officinale* root in transverse section showing all tissues and root regions. The vascular cylinder (stele) has a pith of all parenchyma cells. X50.

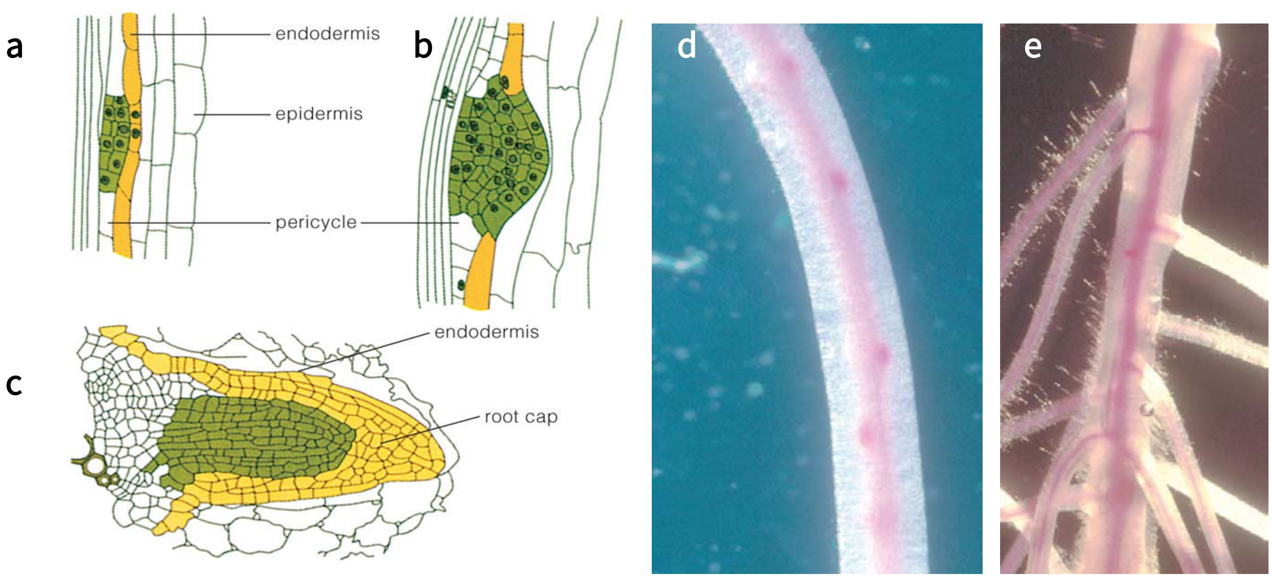


Figure 7.16. Lateral root formation. (a) Initiation of a lateral root of carrot (*Daucus carota*) by division of cells in the pericycle. (b) Formation of the lateral root primordium. (c) The young root pushing through the cortex. (d) Cleared pea (*Pisum sativum*) root showing root primordia. (e) Cleared pea root showing vascular connections of the main axis of the root and the lateral roots.

The Vascular Cambium and the Cork Cambium Partially Form from the Pericycle

In long-lived dicot plants, the older regions of roots form secondary vascular tissues by activating a secondary meristem, the vascular cambium. Secondary growth is initiated by the division of pericycle cells and also some leftover or **residual procambium** cells located between the arcs of xylem and phloem (Fig. 7.17a). Residual procambium cells are actually procambial cells that did not develop into primary xylem or primary phloem. They are now induced to divide, and they form secondary xylem to the inside and phloem to the outside (Fig. 7.17b). After a time, the crescent-shaped region of dividing cells joins with the pericycle, which also begins to divide, forming at least two layers of pericycle cells. The inner layer joins to the residual procambium to form an intact ring of vascular cambium (Fig. 7.17c). The outer layer remains as pericycle.

The secondary xylem or wood in roots with several years of secondary growth looks very much like that of woody stems. The only difference is that in young roots primary xylem occupies the middle of the root (Fig. 7.18a,b), whereas in young stems pith occupies the middle.

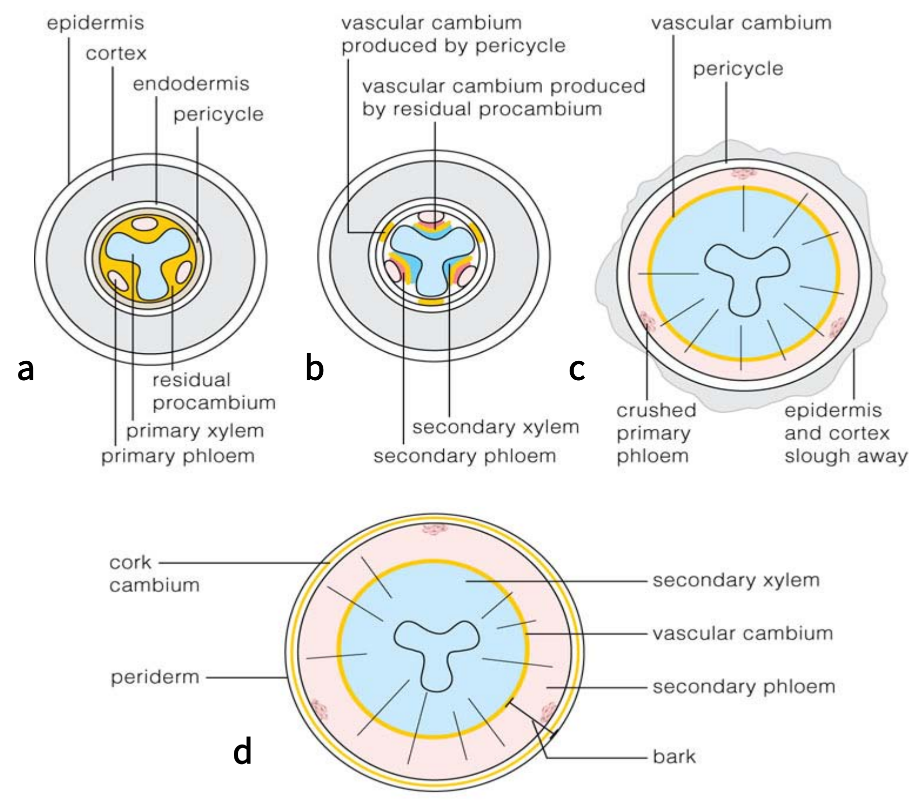
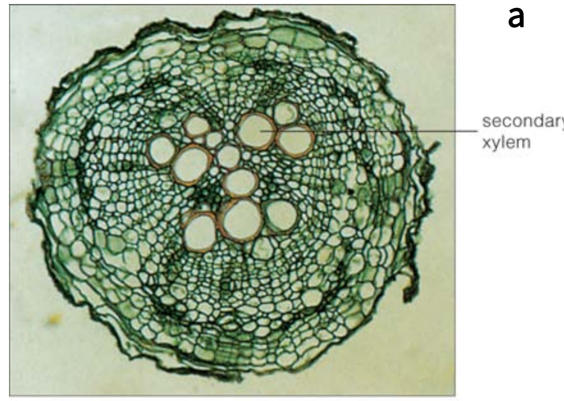


Figure 7.17. Secondary growth in a root. (a) At the completion of primary growth, an arc of residual procambium cells remains between the primary xylem and primary phloem. The pericycle is a complete cylinder. (b) The residual procambium starts to divide and joins with the pericycle cells outside the xylem arms to form a continuous cylinder of vascular cambium. The pericycle just outside the protoxylem points divides to form at least two cell layers. The inner layer joins with the residual procambium to form the vascular cambium; the outer layer stays part of the pericycle cylinder (c) The vascular cambium forms secondary xylem internally and secondary phloem externally. The primary phloem is being pushed outward. (d) A cylinder of vascular cambium produces secondary xylem to the inside and secondary phloem to the outside. The primary xylem remains in the center of the root, the primary phloem has been crushed, and the pericycle that remains will form the cork cambium. The cork cambium forms the periderm after the epidermis and cortex die. The term bark refers to everything outside the vascular cambium.

Continued growth expands the root and finally causes the splitting, sloughing off, and destruction of the cortex and epidermis (Fig. 7.17c). The pressure created by this expansion apparently stimulates the remaining ring of pericycle cells to divide again. This last function of the pericycle converts it into the cork cambium, which forms the periderm (see Fig. 4.20). The bark in woody roots (which includes all cells from the vascular cambium outward) appears similar to that in stems; but it may be thinner and smoother on its outer surface (Fig. 7.17d).

Interestingly, there is only one monocot plant, the dragon's blood tree (*Dracaena draco*), that is known to have secondary growth in roots. Even very tall, tree-like monocots like palms lack secondary growth in roots.

a



b

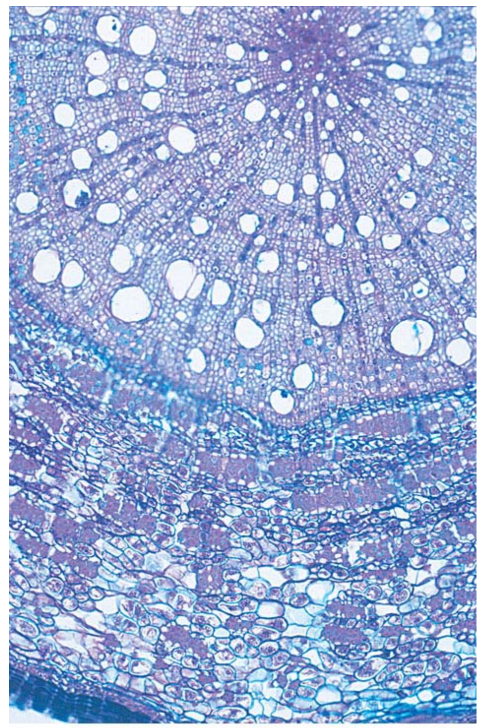


Figure 7.18. (a) Alfalfa (*Medicago sativa*) root transverse section with some secondary tissues and periderm on its periphery. X125. (b) Woody root of oak (*Quercus* sp.). X77.

Some Roots Have Special Functions

Many plants have roots with special characteristics. This chapter has already discussed examples of adventitious roots that arise from non-root origins and the uniquely shaped roots of clinging vines. Other plants, especially those forming partnerships with microorganisms, have specialized root structures. Some important examples are haustorial roots, root nodules, mycorrhizae, and contractile roots.

Parasitic plants like dodder (*Cuscuta* sp.) anchor themselves by sinking **haustorial roots** into the vascular tissue of a host stem, thus tapping the host's water and nutrient supply (Fig. 7.19).

Although nitrogen is one of the most important elements needed by plants, most plants cannot use atmospheric nitrogen (N_2) directly. Certain legumes, such as peas (*Pisum sativum*) and soybeans *(Glycine max*), are capable of fixing nitrogen--that is, changing N_2 that diffuses into the soil into NH_4^+ (ammonium ion), which is usable by the plant. Nitrogen fixation is the result of an unusual relationship between the bacterium *Rhizobium* and the roots of legumes (see Chapter 19; Fig. 19.15). Root cells are infected by the passage of a thin infection thread of the bacteria into root hair cells and on through to the cortical cells. The bacteria then divide and stimulate the cortical cells to divide, thereby forming a **root nodule** (Fig. 7.20). The bacteria are the actual agents for fixing the nitrogen.

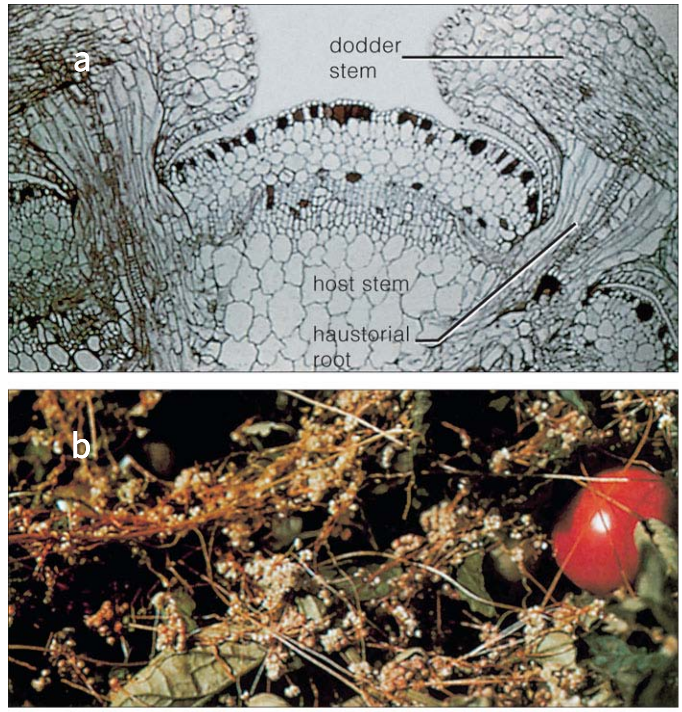


Figure 7.19. (a) Haustorial roots of a plant parasite, dodder (*Cuscuta* sp.) infecting the stem of a host plant, X53. (b) External view of dodder on tomato plants.

Mycorrhizae are short, forked roots common to as many as 90% of seed plants. These specialized root structures represent an association of roots with a soil-borne fungus (see Chapter 20).

Two types of mycorrhizal roots may occur, distinguished by whether the fungus penetrates into the root cells or not. **Ectotrophic mycorrhizae** are found in roots of such trees as pines *(Pinus),* birches *(Betula),* willows *(Salix),* and oaks *(Quercus).* This type causes a drastic change in the root shape (Fig. 7.21), but the fungus does not penetrate the root cells. Instead, the fungus penetrates between the cell walls of the cortex, and it forms a covering sheath (or *mantle)* of fungal hyphae around the entire root. These mycorrhizal roots are about 0.5 cm (0.2 in) long; they lack a root cap and have a simple vascular cylinder. **Endotrophic mycorrhizae** do not form a mantle over the root, and the fungus actually enters the cortex cells (Fig. 7.22). Mycorrhizae make roots more efficient in mineral absorption, but they are apparently not absolutely essential for the growth of the usual host plants (see Chapter 11). This is known because plants that are artificially fed adequate nutrients can grow without mycorrhizae. Mycorrhizae may also be beneficial to their host plants by secreting hormones or antibiotic agents that reduce the potential of plant disease.

Roots of the dandelion *(Taraxacum officinale),* water hyacinth *(Hyacintha orientalis),* and some other plants are capable of contracting, which keeps above ground parts near the soil surface. This contraction is caused by the radial expansion (or, in some instances, the collapse) of cells in the root cortex (Fig. 7.23).

a

b

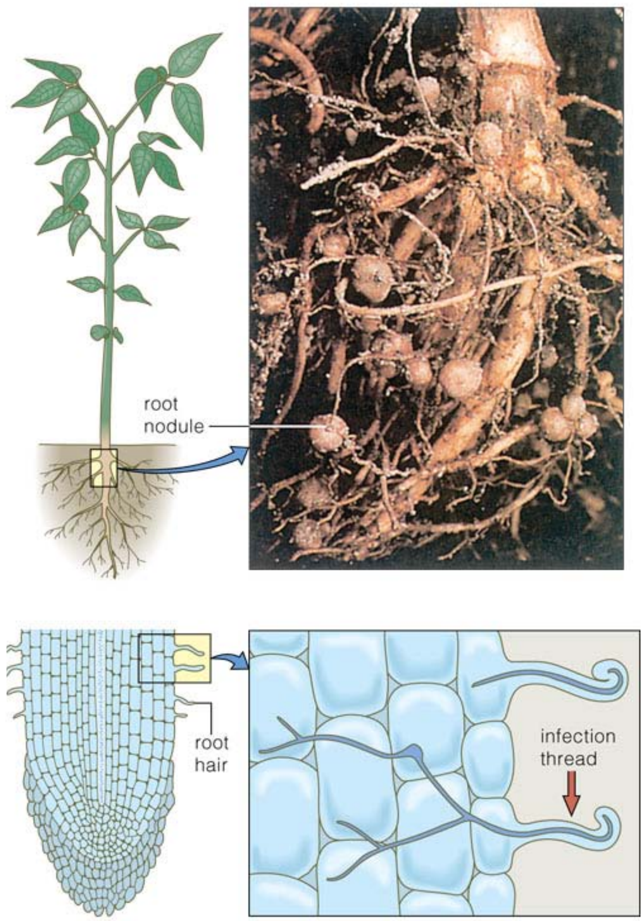


Figure 7.20. Bacterial nodules in legume roots. (a) Legume plants form bacterial nodules on roots. (b) Bacteria enter the plant by passing through a tiny infection thread which penetrates root hairs. Once inside the host, the bacteria penetrate to the cortex of the root forming a swollen mass of cells filled with bacteria. The bacteria, called *Rhizobium* sp., fix nitrogen which then passes up the plant body in a usable form.

a

b

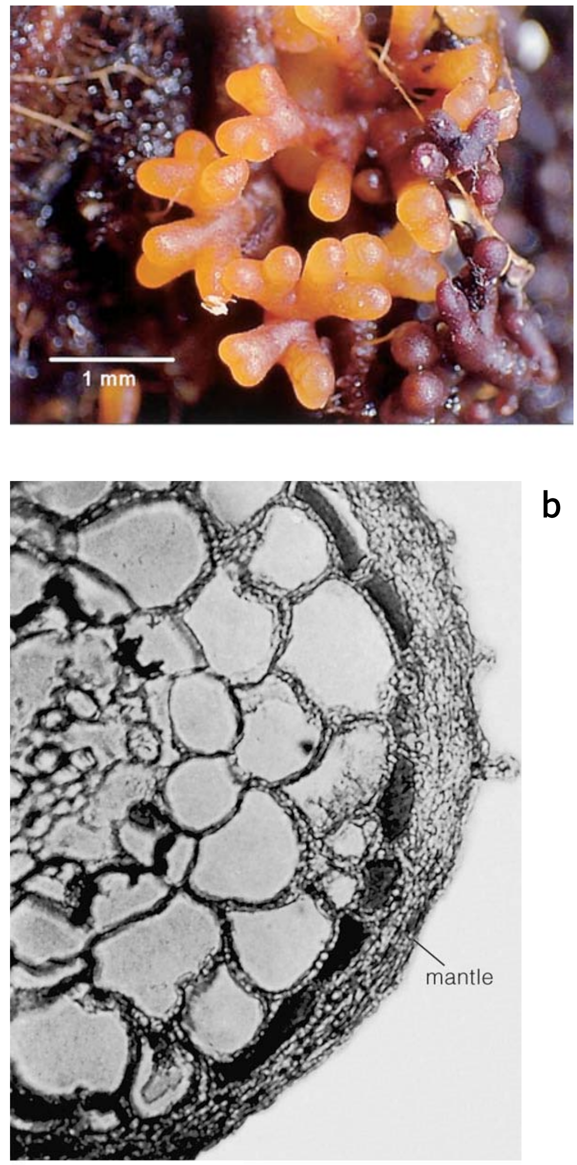


Figure 7.21. Ectotrophic mycorrhizae. (a) The typical Y-branched form in pine roots (*Pinus pinaster*). (line scale = 1mm). (Used with permission from J. Parlade, IRTA-Departament de Proteccio Vegetal, Barcelona, Spain) (b) Transverse section through an infected mycorrhizal root showing the mantle of fungal hyphae, and the hyphae growing between the cortical cell walls, X240.

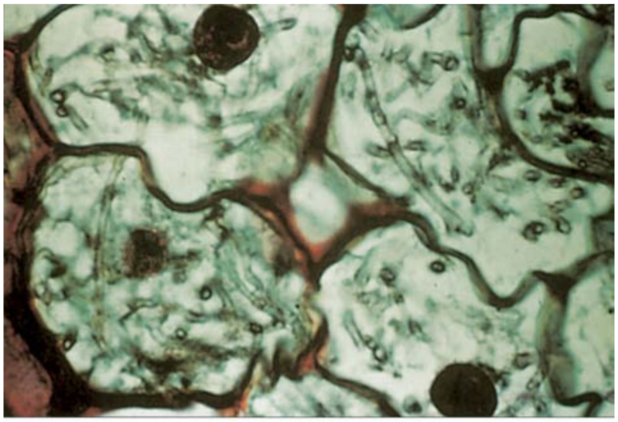


Figure 7.22. Photograph of *Coralloriza* sp. rhizome with endotrophic mycorrhizae, showing fungal hyphae actually inside the host cells. (Note: A rhizome is actually a stem which grows underground. This example is being used, however, because it shows the nature of the infection process very well, and it looks the same in root cells. X735.

Figure 7.23. Contractile roots of water hyacinth (*Hyacinthus orientalis*). Notice the wrinkled surface at the base of these roots where the contraction occurs.

KEY TERMS

adventitious roots
Casparian strip
ectotrophic mycorrhizae
endodermis
endotrophic mycorrhizae
exodermis
fibrous root system
ground meristems
haustorial roots
lateral root primordial
pericycle
pneumatophores
procambium
prop roots
protoderm
radicle
region of elongation
region of maturation
residual procambium
root apical meristems
root hairs
root nodule
seminal roots
tap root system

SUMMARY

1. The principal functions of roots are absorption of water and nutrients, conduction of absorbed materials and food, and anchorage of the plant in the soil.

2. The primary root develops from the radicle in the embryo. It generally penetrates the soil to some depth; if it dominates, a tap root system results, with a main root axis and branches.

3. Fibrous root systems are formed by seminal roots arising in the embryo in addition to the radicle. Grasses are good examples of plants with fibrous roots.

4. Adventitious roots may arise on stems and leaves.

7. The root tip is composed of (a) the root cap, which protects (b) the meristematic region; (c) a region of elongation; and (d) a region of maturation, characterized externally by root hairs and internally by the formation of primary vascular tissues.

6. The epidermis forms as the outer tissue of the root. Water is absorbed through the epidermal cells and the root hairs. The next layer is the cortex. Its cells mainly store nutrients. The endodermis is the innermost cell layer of the cortex. The Casparian strip is a waxy substance found in the radial and transverse walls. Water cannot move across the Casparian strip. Therefore, all water with dissolved nutrients must pass through the protoplasts of endodermal cells. An exodermis is present just inside the epidermis in many roots; it may also have Casparian strips and function in ion absorption and regulation.

7. In cross section, the primary xylem in dicot roots is star-shaped, with protoxylem at the points. Primary phloem arises between the arms of primary xylem.

8. Roots of certain grasses usually have central parenchyma and many protoxylem points.

9. The pericycle, a row of cells internal to the endodermis, represents the outermost row of cells of the vascular cylinder. Cells of pericycle may eventually initiate the differentiation of the vascular cambium and the cork cambium in dicot roots. The pericycle initiates lateral roots in both dicots and monocots.

10. A vascular cambium originates in dicot roots from procambium cells between primary xylem and phloem and from pericycle cells exterior to the radiating points of primary xylem. The vascular cambium forms secondary xylem internally and secondary phloem externally. The resulting increase in diameter stretches and tears the endodermis, cortex, and epidermis. A cork cambium develops from the pericycle and forms the periderm.

11. Haustorial roots from parasitic plants penetrate into the host. Bacterial nodules occur in roots of nitrogen-fixing legumes. Mycorrhizae are roots infected by beneficial fungi. Contractile roots pull the shoot tight to the soil surface.

Questions

1. Identify in a diagram or photograph the following root structures and tissues:

root cap
root apical meristem (RAM)
region of elongation
region of maturation
root hair
epidermis
cortex
endodermis
Casparian strip
pericycle
vascular cylinder (xylem and phloem)

2. State how each item listed in question 1 contributes to the function of the root.

3. Discuss the tissues and cells involved in mineral uptake and transport in a root.

4. Describe the differences between primary and secondary tissues in a root. Where are these located? Make a labeled diagram to show both primary and secondary xylem and phloem.

5. Make a diagram to show the position of cork cambium and vascular cambium in a dicot root.

6. Describe the structure and function of the root cap.

7. Describe two symbiotic associations involving roots (root nodules and mycorrhizae). What are the microorganisms involved, and how does the association alter the structure of the root? How do both partners benefit from the association?

8. Describe two modified roots.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *The climbing fig and its adhesive pads.*

Figure 1. Climbing fig plant (*Ficus pumila*) growing on a privacy wall in Davis, CA.

Everybody has seen vines growing on the sides of buildings and fences. Have you ever wondered how they manage to climb so high and stick to different surfaces?

Climbing vines have developed three different growth strategies– twining, winding and clinging. *Twining* vines like Wisteria (*Wisteria sinensis*) encircle poles and branches by twisting their stems just like winding a rope around a pole. Winding vines like clematis (*Clematis hybrida*) support themselves by tendrils. Tendrils are modified leaves that can twist around poles and other things and attach to them. A third type are called *clinging* vines and English ivy (*Hedera helix*) is probably the best-known example.

Another common plant that uses this strategy is the climbing fig (*Ficus pumila).* Clinging vines climb surfaces by means of clusters of adventitious roots that emerge from internodes and form into an interesting unique and sticky structure called an adhesive pad.

Ficus pumila, the climbing fig, is commonly used as an ornamental to cover walls and fences (Fig. 1). It is a very aggressive plant and it sprouts shoots that rapidly cover almost any surface, including glass windows. Perhaps the first report of the clinging vine mechanism in climbing fig was by Charles Darwin (1875) in his book, *The Movements and Habits of Climbing Plants*. In his report he notes that roots on the stems secreted a "viscid fluid" possibly "India-rubber" that adheres to any surface.

Adhesive Pads Hold the Climbing Fig to Any Surface

The adhesive pad in *F. pumila* develops from a cluster of adventitious roots that are initiated just basal to a node near the tips of shoots (Figs. 2, 3). Adventitious roots are initiated in pairs on either side of a vascular bundle at the second to third internodes of young stems. After emerging through the cortex and epidermis of the stem, the adventitious root clusters elongate until they are a few millimeters long (Fig. 2). The roots then stop elongating, root hairs form on them, and they secrete a very sticky cement substance. The clusters of adventitious roots and their root hairs all stick together forming the adhesive pad (Fig. 3). If the adventitious roots do not touch a substrate they usually dry up; if they touch moist soil they tend to branch and change to a terrestrial form. If you ever see a climbing fig try pulling one away from the wall; you will see how strongly they stick.

Fig. 2

Fig. 3

Figure 2. Tip of a climbing fig branch showing the position of an adhesive pad (red circle).
Figure 3. Close up view of an adhesive pad taken through a glass plate. Note that some of the adventitious roots have merged and some are separate. Hairs on the surfaces of these roots secrete a sticky substance that glues the pad to any surface.

PLANTS, PEOPLE, AND THE ENVIRONMENT: *Myths and Popular Uses of Roots*

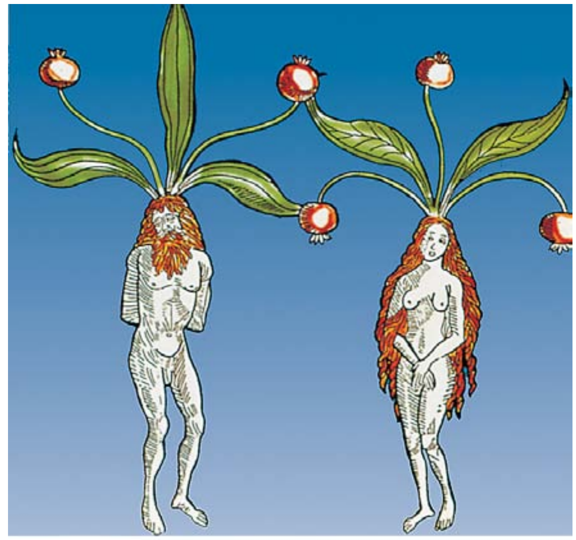


Figure 1. These are colored drawings of mandrake plants originally from an old German Herbal. Herbals were among the very first books ever made. They contained drawings of plants and sometimes discussed how they could be used. (From Lewis, W.H. and M.P.F. Elvin-Lewis. 1977. Medical Botany: Plants Affecting Man's Health. Wiley-Interscience. N.Y. Used with permission of Wiley-Interscience.)

Over the millennia, through trial and error, ancient peoples developed traditional uses--medical and otherwise--for berries, seeds, leaves, stems, and roots. Much of this plant lore has little validity in medical fact, but some traditional plants have proven to be effective remedies.

During the Middle Ages in Europe, most people believed that the way a plant looked (its shape or color), how it smelled, or some other characteristic provided clues about its uses for people. This was called the Doctrine of Signatures. For example, the roots of the mandrake (*Mandragora officinarum*, Fig. 1) are thick and fleshy and tend to be irregularly branched; with a little imagination the shape of a person could be seen in a root carefully extracted from the soil. In the Middle Ages, people assigned considerable importance to the manlike appearance of these roots; they believed that such roots could bring good fortune. In some cases the roots were even ground up and eaten as a love potion. Mandrake root doesn't seem to have much real medicinal value. It doesn't really give anyone good luck, and it certainly doesn't work as a love potion; but in some cases an infusion made from mandrake root may help control a cough.

Another root that looks vaguely like a person is the ginseng (*Panax quinquefolium*). In Asia, ginseng root has been considered a cure-all for many ailments. Ginseng also grows in the United States, but it has only recently become popular. Nowadays you can find it in most health food stores. Most likely, the subtle, supposedly restorative power associated with ginseng is psychological: it helps because you think it will. However, some recent evidence suggests that chemicals in ginseng roots do act to calm some people.

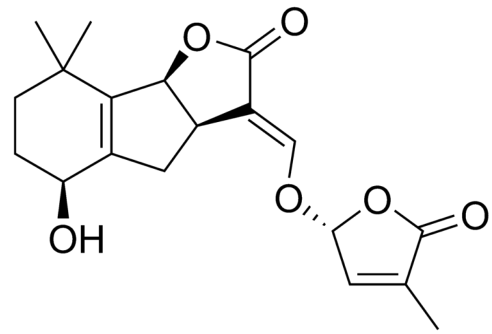
A root with more widely accepted utility comes from the cassava (*Manihot esculenta*), a shrubby South American plant. The whitish latex that exudes from a cut plant contains hydrocyanic acid, a deadly poison used by Brazilian Indians to make poisoned arrows. The interesting thing, however, is that when the latex is removed, the rich, starchy pulp is a good food source. Native people ground up cassava root, placed it in a sack, and hung it from a tree; when all the juice dripped out, the meal that remained could be made into cakes and eaten. It was called farina. Now cassava is grown commercially. You are probably familiar with the starch-rich pellets manufactured from cassava root, called tapioca.

Native Americans also have a rich plant lore that includes roots. The roots of several plants were used as a source of soap. One of these--soap weed (*Yucca* sp.)--is now used as a component of popular shampoos. *Yucca* root juice was also used as glue to fasten feathers to arrows. One type of soap root was used to induce vomiting as a step in ritual purification ceremonies. Another type was thrown in streams to stupefy fish so that they could be harvested without using fishing gear. Roots are obviously important to the plant, but many also have uses for people

IN DEPTH: How Do Roots Advertise their Presence?

Certain connections between plant roots and fungi are extremely important for both members. In a mycorrhizal association, fungi get a rich source of carbohydrates, which provide carbon and energy for growth. Plants get a source of inorganic nutrients. Phosphate is particularly important, since phosphates have very limited solubility in soil solutions. But how does the association form? How do the two members find each other? Is it just random chance?

Recent research has identified a class of compounds, strigolactones (right), synthesized in the roots of all plants. These compounds serve to control growth in plants--they tend to inhibit branching in shoots--but they are also exuded from roots and can serve as a signal to attract mycorrhizal fungi [particularly ascomycete fungi (see Chapter 20) that form arbuscular mycorrhizae]. Strigolactones tend to break down in the soil, so that there is a gradient of concentration, dropping steeply away from the root (or from the fungus's standpoint, rising steeply as it grows toward the root).



The name "strigolactone" is derived from the plant genus *Striga* (witchweed), reflecting an unfortunate side-effect of the exudation of these compounds. *Striga* is the genus of several species of parasitic plants. *Striga* seeds germinate and form a root-to-root connection with a nearby plant, for instance maize or sugar cane, removing carbohydrate and other nutrients from the host plant and eventually killing it.

Strigolactones stimulate the germination of *Striga* seeds. And just as mycorrhizal fungi zero in on roots by detecting the gradient of strigolactones, so may *Striga* roots.

Right: *Striga* (witchweed) plant (photo by Randy Westbrooks, Invasive Plant Control, Inc., Bugwood.org)

For more information: http://www.biomedcentral.com/17417007/12/19

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Figure 7.16 d & e = photo of root cleared to show cont. vascular connection – Maude Hinchee
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Figure 7.21 a = ectotrophic mycorrhizae- typical Y-branched from in pine roots - Used with permission from J. Parlade, IRTA-Departament de Proteccio Vegetal, Barcelona, Spain)
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Sidebar – *Ficus pumila* – Figures 1-3 – Thomas L. Rost