10

Roots

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Introduction

The function of modern-day roots has not essentially changed from their early evolutionary development, i.e., the uptake of water and minerals as well as anchorage for the stabilization of shoot development and growth, but also food storage, the production of plant growth regulators, and aeration. Roots have an anatomy that is distinctly different from that of shoots, as dictated by the substrate in which they grow—air vs. soil. Stems have nodes from which they can produce stems, leaves, flowers, or roots. Roots lack nodes and can only produce lateral roots. The root cap protects the growing tip as it pushes through the soil. Lateral roots originate from the interior of the root, some distance from the tip, as opposed to leaf initiation which is from the shoot tip. Roots adjust their growth in response to gravity, water, and nutrition. They are insensitive to light, unlike the very light-sensitive shoot. Root vasculature is characterized by a central, often solid in eudicots and pithy in monocots, mass of xylem surrounded by individual patches of phloem. Symbiotic associations with certain bacteria and fungi greatly enhance nutrient acquisition and uptake.

10.1 Roots and Root Systems Serve Multiple Purposes

Roots have multiple functions. Roots anchor plant to the substrate, even in the most precarious situations (◘ Fig. 10.1a). The epiphytic strangler figs start as a germinating seed on a limb or trunk and grow their roots down to the soil, completely encircling the host plant (◘ Fig. 10.1b). The host plant is only used as a source of support; no water or nutrition is derived from it by the strangler fig. Roots of many plants maintain a role in the storage of nutrient substances, many of which serve as a source of foods for animal and human needs. Beetroot (*Beta vulgaris*), carrot (*Daucus carota*), parsnip (*Pastinaca sativa*), radish (*Raphanus sativus*), and sweet potato (*Ipomea batatas*) are but a few major root crops. While most of these nutrients are carbohydrate, some roots store oils, proteins, and fats as well as mineral nutrients such as phosphates and sulfates. Horseradish (◘ Fig. 10.1c) stores irritating chemical compounds that serve as an anti-herbivory defense and a spicy flavoring. Stored carbohydrates are important in non-crop species for stem regeneration after heavy pruning (Vriet et al. 2014) and in the production of leaves and flowers by fruit trees in the spring (Tromp 1983). Succulent roots store water in large parenchyma cells (Hearn et al. 2013), in a manner analogous to that found in succulent leaves (► Sect. 12.7). Plants growing in wet or marshy areas, such as mangrove (◘ Fig. 10.1d), put out a large number of adventitious "**prop**" roots that contain a large amount of internal aerenchyma. The roots both provide support and help aerate those portions of the root system that are submerged in the low oxygen substrate (Purnobasuki and Suzuki 2005).

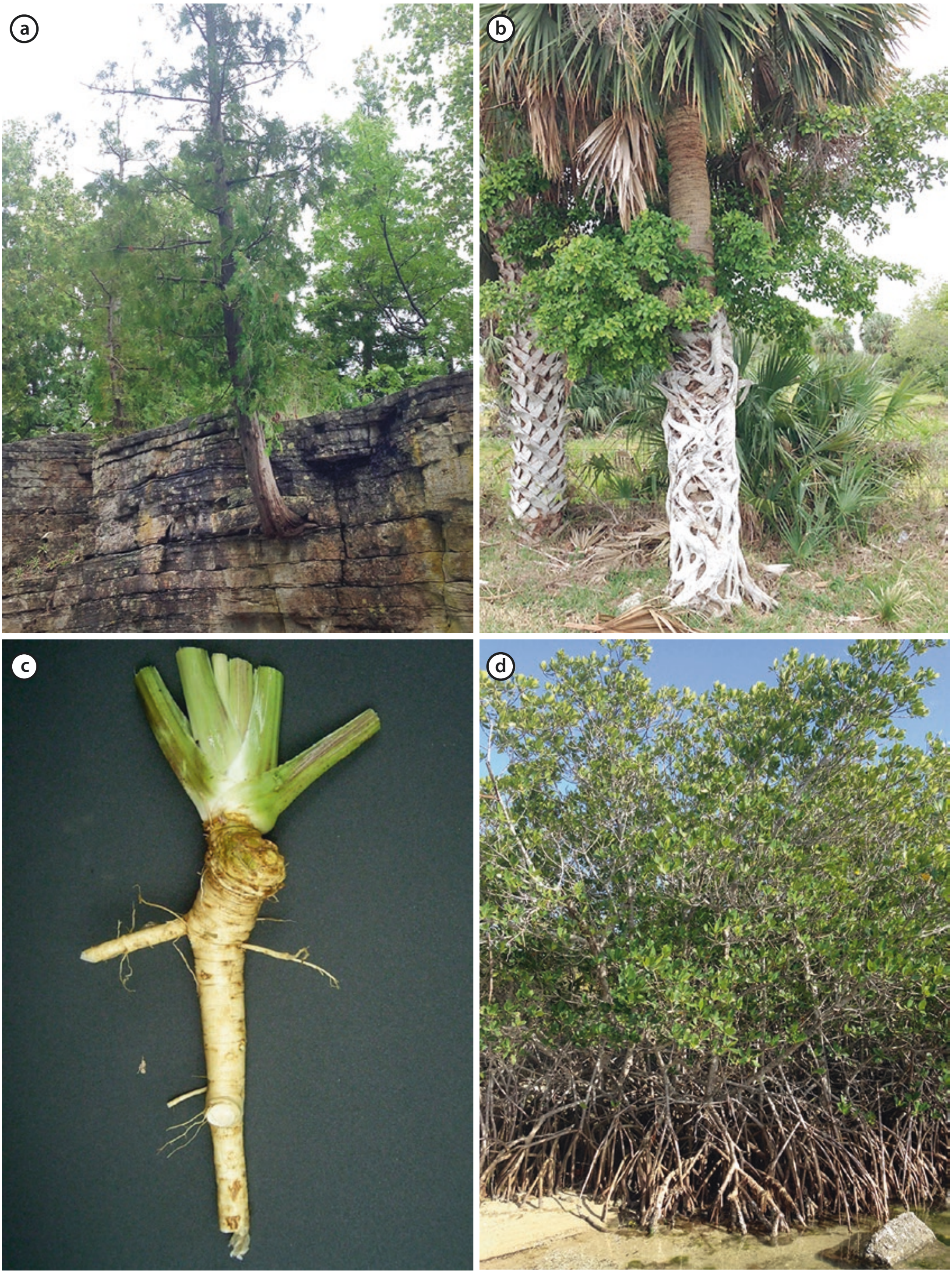


Fig. 10.1 **a** White cedar (*Thuja occidentalis*) anchored to a cliff face by its root system. **b** Strangler fig (*Ficus banyan*) roots wrapped around a palm. The fig leaves are at the top of the root system, about halfway up the palm trunk. **c** Horseradish (*Armoracia rusticana*) storage root, harvested and with most of the leaves cut off. **d** Red mangrove (*Rhizophora mangle*) prop roots. (**a**, **d** RR Wise; **b** JJ Wise; **c** F Vincentz, CC BY-SA 3.0)

Nongreen parasitic plants that lack the chlorophyll necessary for photosynthesis must develop parasitic growths called **haustoria** (threadlike growths of a parasitic plant), which enter into the water- and food-conducting tissues of a host plant in order to obtain their nutrition (◘ Fig. 14.7a). This requires a fusion of the vascular systems of the host and parasite and is discussed in ▶ Chap. 14—Vascular Cambium.

Although it might be most convenient to view plant anatomy as a series of structural/functional parts, nevertheless one should not lose sight of the fact that plants represent integrated systems just as in the case of all living organisms. To this end, while unique in many ways, the organs of a plant must communicate with each other to produce a viable and successful organism. Employing molecular physiology, we are starting to learn more about the reciprocal exchange of information and needs of plants. Thus, roots and shoots exchange plant growth regulators (a.k.a. hormones) which carry such information to provide for growth, differentiation, and resistance to herbivory (Jackson 2002; Takei et al. 2002). The risk of herbivory varies from one part of the plant to another. For example, roots are less likely to be attacked by insect herbivores than leaves, whereas leaves have a far lower likelihood of threat from fungi, bacteria, and nematodes than subterranean roots. Changes in plant growth regulator levels are significant in repair to structural damage in root tips and shoot apical meristems to bring about repair and renewed growth. Following herbivore damage such regulators as abscisic acid, auxins, cytokinins, ethylene, and gibberellins are believed to play key roles in communication trafficking and in directing appropriate repair (Kaplan et al. 2008).

Water uptake represents one of the primary functions of roots. The amount of water taken up per plant community or individual plant for transpiration varies tremendously based on a host of factors (including the method used to measure that water movement). In an extensive literature survey, Wullschleger et al. (1998) reported water usages on a per plant basis ranging from the low teens to several hundred kg H_2O day^{-1}. *Eperua purpurea*, a tropical tree in the Leguminaceae, topped the list with a value of 1180 kg H_2O day^{-1} or over 300 gallons a day.

While mineral nutrient uptake may typically follow the same passive pathway as water in root systems, in many cases the plant **root hairs** and surface cells may expend energy in order to take up and concentrate mineral ions. This includes minerals such as nitrates, phosphates, and potassium which cannot be absorbed across the plasma membrane without such a chemiosmotic force. Nitrogen enters the root as nitrate (NO_3^-) or as ammonium ions (NH_4^+), whereas phosphorus enters as PO_4^{3-}, calcium as Ca_2^+, and potassium as K^+. Inorganic ions pass from cell-to-cell through plasmodesmata for the most part, but from the cytoplasm of the pericycle cells (just inside the endodermis) to the xylem transport is mostly by means of active transport. When incorporated into the xylem of roots, minerals may exit and enter cells that require them.

Water and ions are taken up from the soil, move radially through the cortex to the stele (a.k.a. **central cylinder**), and then

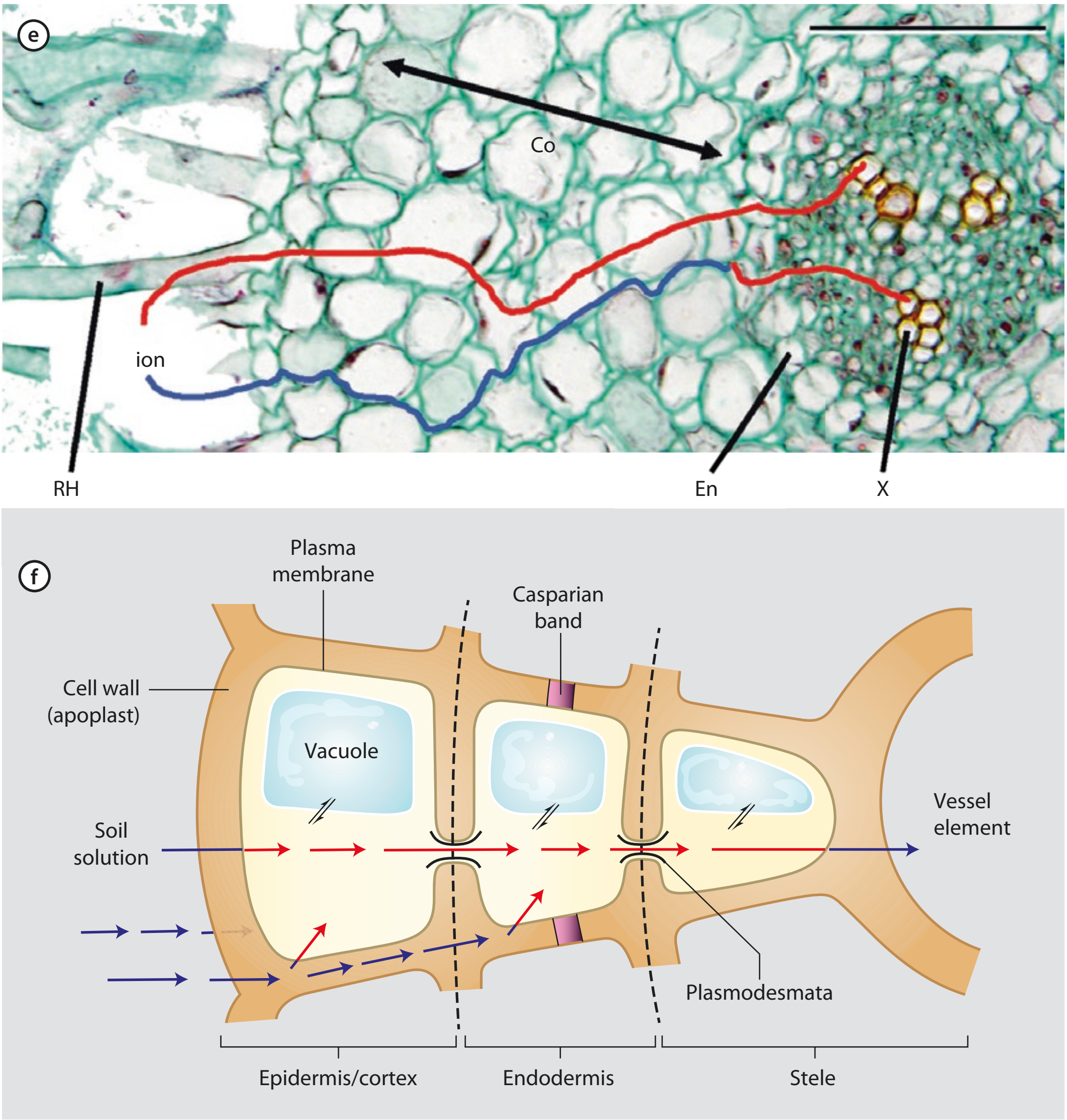
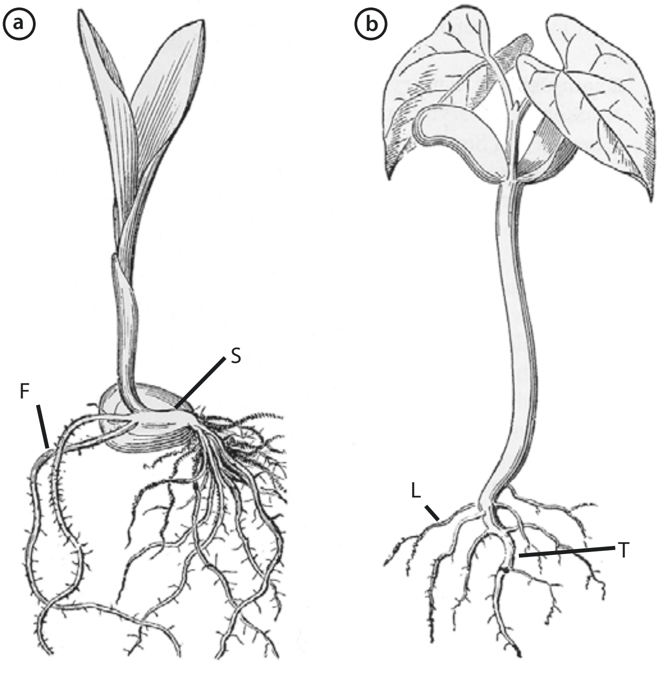


Fig. 10.1 **e**, **f** Water and ion uptake by plant roots may take a symplastic pathway (red arrows) or an apoplastic pathway (blue arrows) from the soil water, through or around the root hair (RH), cortex (Co), to the endodermis (En). The Casparian strip in the endodermis forces apoplastic water and ions to cross the plasma lemma and enter the symplast of the endodermis from which they then move via plasmodesmata into the xylem tracheary elements (X) in the stele. Scale bar in **e** = 50 µm. (**e** RR Wise; **f** redrawn from Crang and Vassilyev 2003)

move in an axial direction to the shoot. Figure 10.1e, f shows the two anatomical pathways of water and mineral ion uptake in roots. When following the **symplastic pathway**, water and mineral ions move across the root hair plasma lemma and immediately enter the root hair cytoplasm. They then travel cell-to-cell via plasmodesmata through the cortex, endodermis, and into the living parenchyma cells of the stele. Ion uptake requires an energy source (ATP or membrane potential) and specific membrane-bound transport proteins, the presence and permeability of which are under control by the cell. The plant, therefore, has the ability to exclude or concentrate certain ions. The "decision" on which ions the plant takes up is made at the root hair. In the **apoplastic pathway**, water and ions passively enter the cell wall space of the cortex and diffuse to the cell wall space of the endodermis. There, the **Casparian strip** (refer to ► Sect. 10.1) blocks further apoplastic movement, and the ions must be transported across the plasma lemma of the endodermal cells to enter the symplasm and move on to the stele. In this case, the "decision" on which ions the plant takes up is made at the endodermis.

10.2 Root System Morphology Is Diverse and Adapts to Soil Conditions via Compensatory Growth

Root morphology may be largely classified into two groups. Monocots typically produce a fine but dense network of roots termed a fibrous root system (◘ Fig. 10.2a). Fibrous roots, most typical of grasses, do not grow as deep into the soil as taproots and usually are found where water and phosphates are more abundant and thus grow more in a horizontal pattern. Fibrous roots also often form a complex with soil particles that aids in the prevention of erosion. Eudicots, on the other hand, mostly possess a taproot system (◘ Fig. 10.2b) in which the primary root grows downward in the soil and develops smaller lateral roots. Such taproot systems are often found in dry soils and grow deep toward underlying water

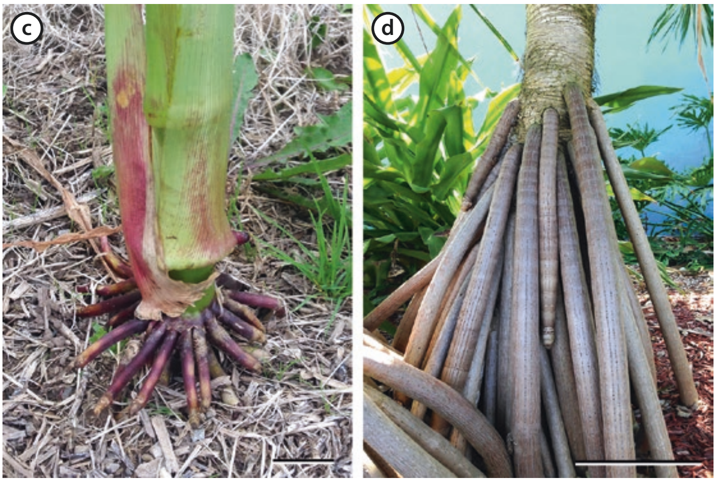


◘ **Fig. 10.2** **a**, **b** Drawings of **a** maize (*Zea mays*-monocot) and **b** bean (*Phaseolus vulgaris*-eudicot) seedlings. F, fibrous root; S, stem; L, lateral root; T, taproot. Scale bars = xx µm. (**a**, **b** A Grey (1887), public domain) and nitrogen sources. The fact that the last tracheophytes to arise, namely, the eudicots, have a taproot system and the ferns have fibrous systems indicates that the fibrous root system evolved first. The fibrous/tap distinction may be lost in perennial plants such as trees as the root system develops and adapts to local soil conditions.

During seedling germination, the first organ to develop from both monocots and eudicots embryos is the **radicle** (refer to ► Chap. 19). In eudicots, the radicle continues to elongate, develops an apical meristem and root cap, and becomes the taproot from which lateral roots subsequently arise.

Development of the monocot root system is more complicated. Maize is a prototypical annual grass. Maize produces two root systems. The first includes the radicle and a series of 3–6 seminal roots. Seminal roots are adventitious lateral roots that arise from the embryonic stem. At germination, a true root develops from the radicle, and the seminal roots elongate. Together, they are called the primary root system and are only present during early seedling development. The secondary root system is composed of adventitious roots that arise later from nodes higher on the developing shoot, some from nodes below the ground and some from nodes above ground. Those roots arising above ground are called prop roots (◘ Fig. 10.2c). Prop roots can be quite extensive, as can be seen in screw pine (◘ Fig. 10.2d). The maize primary root system aborts after the first few weeks of growth and after the secondary root system has become established. Therefore, all the roots on a mature maize plant are adventitious. Typically, adventitious roots are the sole source of roots in vegetative propagation in which sections of rootless stem tissue are induced to grow roots from existing nodes (Steffens and Rasmussen 2016).

Roots show compensatory growth inasmuch as the architecture is not stable. Roots also respond almost exclusively to variations in soil texture, moisture, nutrients, aeration, and biota. Roots are



◘ **Fig. 10.2** **c** Secondary, adventitious roots arising from a maize (*Zea mays*) stem at a level above the soil. **d** Adventitious roots of screw pine (*Pandanus utilis*) growing from the stem. These new roots serve a primary function of stabilizing the plant in strong winds or during heavy rain spells. Scale bars = 2 cm in **c** and 20 cm in **d**. (**c**, **d** RR Wise) also subject to additional possible abiotic stresses such as drought, flooding, salinity, and extreme temperatures. We are learning that root system defenses to such stresses involve anatomical, cellular, and molecular mechanisms.

Box 10.1 Root Hydrotropism Involves the Action of ABA in the Root Cortex

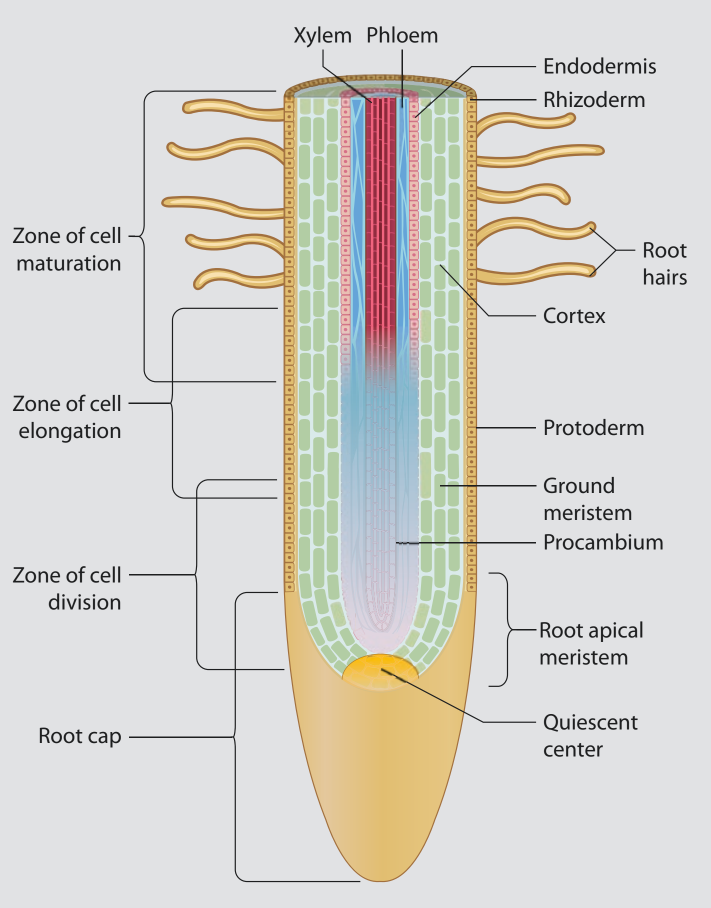
Tropisms are growth-driven movements. Phototropism, seen almost exclusively in shoots, is growth toward or away from light. Gravitropism, found in both roots and shoots, is growth toward or away from gravity. Hydrotropism is growth of the root tip toward soil water, allowing roots to actively seek out areas of the soil that contain more moisture. Phototropism and gravitropism have been well studied. Indeed, Charles Darwin performed the first phototropism experiments in the 1800s. Both the plant hormone (auxin) and tissues involved (endodermis, root cap) have been well-defined for both tropic responses. However, until recently, the signaling pathway for hydrotropism was virtually unknown other than the knowledge that abscisic acid (ABA) was involved, not auxins. In a series of elegant experiments, Dietrich et al. (2017) have elucidated the role of ABA in hydrotropism and identified the root cortex as the tissue wherein the physiological response takes place. First, they used laser ablation (which kills cells) and surgical excision to demonstrate the root cap is not involved in hydrotropism. Second, they used mutants lacking the hydrotropic response to probe which genes are active in which tissues during hydrotropism. The ABA signaling pathway is known to follow these steps: ABA inhibits a class of receptor proteins known as PYR/PYL/RCARs. When active, those proteins suppress the activity of PP2C kinases. The PP2C kinases would normally dephosphorylate, and inactivate, SnRK2s, which activate transcription factors, leading to a growth response. In the presence of ABA, therefore, SnRK2 activity is maintained, and the growth response proceeds. Gene constructs of known ABA signaling proteins and tissue-specific promotors were then used to "turn on" the response in the root cap, epidermis, endodermis, or cortex. Hydrotropism was only restored in the mutants when the cortex signaling pathway was activated, thus demonstrating a tissue-level location of the hydrotropism response very different from that for phototropism and gravitropism.

Reference: Dietrich et al. (2017).

In the monocot families Asphodelaceae, Agavaceae, and Cactaceae and a few herbaceous perennial eudicots, the major roots have the capability of undergoing a contraction of length after establishment. Such roots are termed **contractile roots** and are often responsible for pulling the plant deeper into the soil and protecting the plant from excessive sun and heat, as described for the “living rock” plant (Garret et al. 2010). In contractile roots, the radial longitudinal walls not only shorten but become thicker in the process of contraction. The process of shrinkage may take several weeks but may account for as much length contraction as 50%.

10.3 Primary Growth of Roots Involves Formation of Tissues and Their Organization

The root apical meristem is the source of new cells for the root (► Sect. 4.11), and ◘ Figure 10.3a shows the relationship of the RAM to the tissues of the primary root. The RAM generates the daughter cells that become the three other root meristems. The procambium produces the vascular tissues of xylem and phloem, the protoderm produces the rhizodermis, and the ground meristem produces the cells of the cortex. The growing root tip may be further



◘ **Fig. 10.3** **a** Diagram of a root tip. The root cap and three zones of differentiation (division, elongation, and maturation) are labeled to the left. The four meristems (RAM, procambium, ground meristem, and protoderm) are labeled to the lower right. The six mature tissues (cortex, root hairs, rhizodermis, endodermis, xylem, and phloem) are labeled to the top right. (Redrawn from Crang and Vassilyev 2003) divided into four zones – the root cap (treated further in ► Sect. 10.4), the zone of division, the zone of elongation, and the zone of maturation.

The zone of division (which arises directly from the RAM) is just behind the root cap and generates cells of both the root cap and the root proper. While it may be largely a semantic distinction, the RAM may be thought of as the quiescent center (► Sect. 4.11) and its immediate, undifferentiated daughter cells. Those products subsequently differentiate into the protoderm, procambium, and the ground meristem, and it is those three meristems that make up the zone of division. If physical damage occurs to the quiescent center, or if it is nutritionally stressed, root tip growth may be arrested or (with partial damage to the quiescent center) abnormal growth may occur (e.g., forked development). Cells that are active in division are essentially isodiametric cubes with large nuclei, but with few and small vacuoles. A central pith tissue is developed in grasses and many other monocots but is not normally found in eudicot plants because of compression forced by the establishment of the central **vascular cylinder**.

At the upper end of the zone of cell division (i.e., toward the stem) is a gradual change into a zone of elongation. True to its name, cells in this zone undergo elongation prior to full differentiation, and this elongation is responsible for an increase in length of the root. Little to no secondary cell wall is laid down yet, and the cells do not function in water or ion uptake.

The zone of maturation is where differentiation of tissues takes place, involving vascular tissues, cortical parenchyma, and the rhizodermis. Stele formation begins with the maturation of primary xylem, primary phloem, and the endodermis allowing for the uptake, and transport, of water and ions. Root hairs, which play a critical role in water uptake (► Sect. 10.5), begin to appear. Root hairs can only develop after root elongation has ceased, or else they would be torn off as the root advanced through the soil. The growth of root hairs greatly increases the area of the root allowing for efficient uptake of water and mineral substances (Grierson et al. 2014), which can be delivered to the stele.

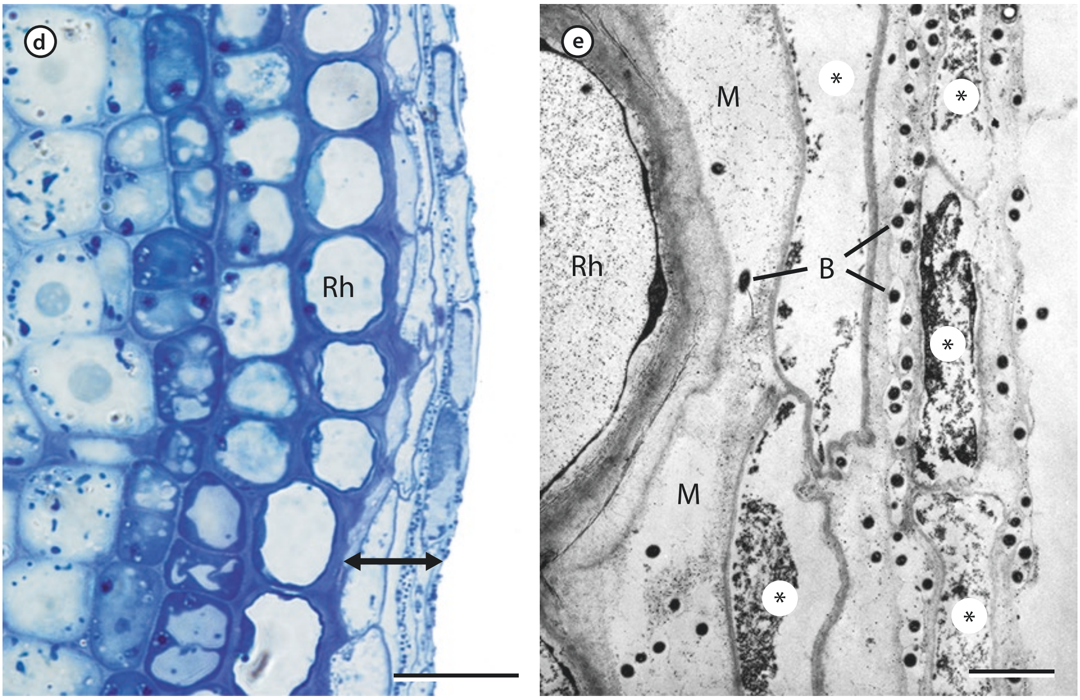
10.4 The Root Tip and Root Cap Control Rate and Direction of Root Growth

The early developing root that grows from a root apical meristem is protected by a renewing coat of terminal parenchyma cells designated as a **root cap** (◘ Fig. 10.4a–c). The origin of the root cap from the root apical meristem is described in ► Sect. 4.11.

In floating aquatic plants such as duckweed (◘ Fig. 10.4a), the root cap is quite distinct from the root tip, the only point of contact being at the tip of the root, which is where the root cap cells are generated. Duckweed (*Lemna* sp.) is a floating aquatic plant, and its root cap is a reasonably stable structure because it is not worn away by soil abrasion. In other plants, the root cap may be less evident and tightly adhered to the root tip (◘ Fig. 10.4b, c).

◘ **Fig. 10.4** **a**–**c** Root tips with root caps. **a** The duckweed (*Lemna* sp.) root cap, seen in longitudinal section, is easily distinguished from the root tip. **b** Longitudinal section of pea (*Pisum sativum*) root tip and **c** SEM of thale cress (*Arabidopsis thaliana*) root tip. The terminus of the pea root tip (RT) is shown by the black line in **b,** and the upper extent of all three root caps is indicated by single-headed arrows. Scale bars = 100 µm in **a** and **b** and 50 µm in **c.** (**a**–**c** RR Wise)

The zone of division encompasses the protoderm that becomes the rhizodermis (a.k.a. epidermis) of the root, the ground meristem that develops into the cortex, and the procambium that in turn produces primary xylem and phloem. The outer root cap cells produce a slimy substance called **mucigel** via **exocytosis** from numerous dictyosomes that traverse the cell wall and pass to the outside surface of the root. The mucigel lowers friction between the root and soil particles during root growth and contains root cap cells that have been sloughed off (◘ Fig 10.4d). Those cells maintain a living protoplasm even after detachment from the root cap but eventually are lost and die. Mucigel is a lubricating product composed primarily of glycoprotein-rich compounds and pectins. It also contains carbohydrates and proteins that aid in the support of bacterial growth (◘ Fig. 10.4d, e). The mucigel/microbe/rhizosphere is an ecosystem in and of itself that benefits both the plant and the microbes (York et al. 2016).



◘ **Fig. 10.4** **d** LM of the margin of a sweet potato (*Ipomea batatas*) root tip. The root cap cells and mucigel (double-headed arrow) lies to the outside of the rhizodermal (Rh) of the root proper. **e** TEM of bacteria in mucigel of sweet potato root tip showing one large rhizodermal cell (Rh). Five root cap cells are indicated by (*). Numerous bacteria (B) are scattered throughout the mucigel (M). Scale bars = 10 µm in **d** and 2 µm in **e**. (**d**, **e** RR Wise)

Gravity is one of the major environmental cues sensed by roots. Positive **gravitropism** describes growing in the direction of the gravitational vector, i.e., down. The embryo has a definite shoot end (plumule) and root (radicle) end (refer to ► Chap. 19). During germination, the radicle emerges first and grows down (◘ Fig. 10.4f), with the shoot emerging slightly later. If the seed is germinated with the radicle pointing up, the root still grows down, and the shoot (lagging behind) grows up (◘ Fig. 10.4g). A seed germinated in the upright position develops normally, but when oriented perpendicular to gravity, senses the change and once again grows downward (◘ Fig. 10.4h).

Gravisensing takes place in the **columella**, a region of specialized cells at the center of the root cap (◘ Fig. 10.4i). Cells of the columella have a large number of amyloplasts (◘ Fig. 10.4j). As described in ► Sect. 3.5.4, amyloplasts are starch-containing plastids. For the vast majority of amyloplasts in a plant, the stored starch, upon remobilization, represents a major food source for both plants and animals because starch is a polymer of high-energy glucose monomers. Starch is also heavy, and the amyloplasts in the columella sink, or settle, in response to the gravitational vector. Therefore, the amyloplasts of the columella are usually referred to as **statoliths**, meaning "static rock," to differentiate them from those amyloplasts that function exclusively in starch storage. Likewise, the statolith-containing cells of the columella are termed **statocytes** to highlight their function in gravisensing.

◘ **Fig. 10.4** **f**–**h** Maize (*Zea mays*) seeds germinated while facing different gravitational vectors. **f** Seed was positioned with radicle end pointed down, toward the gravitational vector. The root (R) grew toward gravity (down), and the shoot (S) grew away from gravity (up). Note that the root, which started growing first, is longer than the shoot. **g** The seed was germinated with the radicle end pointed up. The root grew up until it developed a root cap, then it sensed gravity and grew down. The shoot grew up. **h** Germination was started with the seed radicle pointing down, as in **f**. After 4 days, the seed was rotated 90° counterclockwise. The root grew down (to the right) initially, then changed direction upon reorientation of the seed. Scale bar = 1 cm. (**f**–**h** RR Wise)

The change in growth direction seen in ◘ Fig. 10.4h can be followed experimentally. When a plant is positioned on its side, such that the root tip is perpendicular to the direction of gravity, the statoliths sink to the new bottom cell wall. In a short time (e.g., a few hours), the shoot or root will show growth in the new vertical direction (refer to ◘ Fig. 10.4a–c). In *Arabidopsis* sp., laser ablation of the central columella cells with the most amyloplasts caused the strongest inhibitory effect on root bending (Blancaflor et al. 1998). When amyloplasts settle to the bottom of the gravity-sensing cells in the columella, they physically contact the endoplasmic reticulum (ER). This causes the release of calcium ions from inside the ER. Such calcium signaling in the cells in turn brings about polar transport of the plant hormone indole acetic acid (IAA) to the bottom of the cell. Polar IAA transport from cell-to-cell is mediated by transmembrane transporters. In roots, a high concentration of IAA inhibits

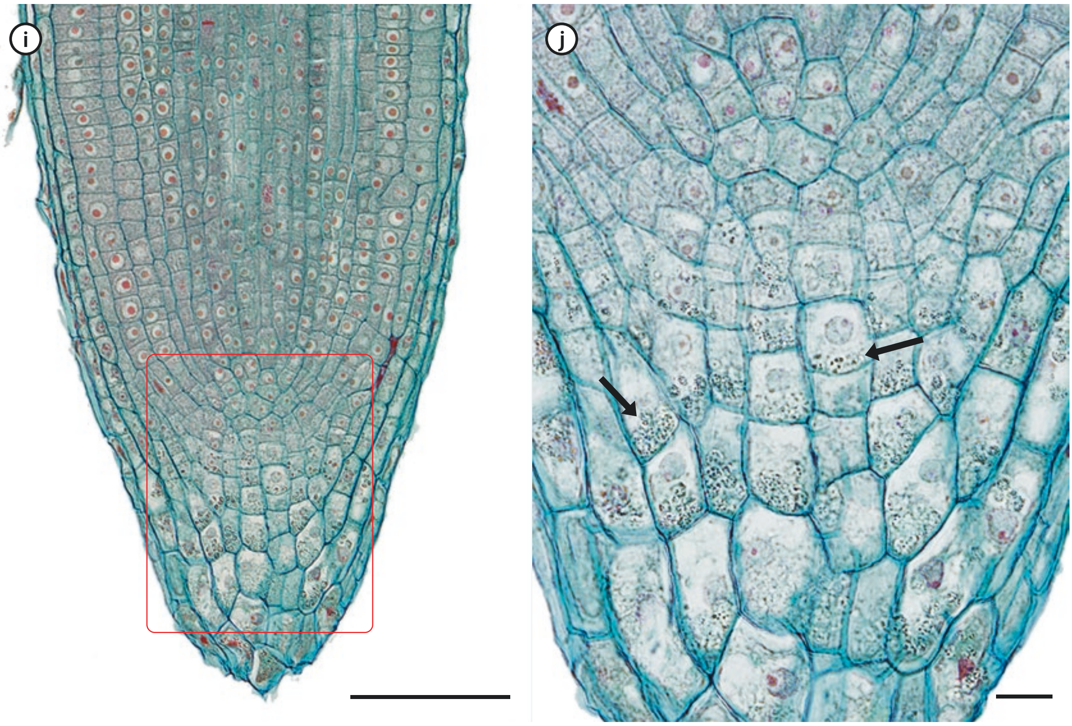


Fig. 10.4 **i, j** Tomato (*Solanum lycopersicum*) root tip in longitudinal section. **i** The red box indicates the area of Figure 10.5. It includes the bottom of the root tip and the region of the columella. **j** Starch-containing amyloplasts (arrows) have settled to the bottom of the columella cells. Scale bars = 50 µm in **i** and 5 µm in **j**. (**i, j** RR Wise)

cell elongation. The effect slows cell elongation on the lower side of the root, while cells elongate normally on the upper side resulting in positive gravitropism. IAA has the opposite effect in shoots, where a higher concentration at the lower side of the shoot stimulates cell expansion and causes the shoot to grow upward (negative gravitropism). The role of the shoot endodermis in negative gravitropism is described in the Stems Chapter, ► Sect. 11.5.

The growth phenomenon described above results in positive gravitropism. However, not all roots grow straight down. In secondary, tertiary and higher-order lateral roots, the root cap senses the gravitational vector per normal but directs a different growth response. Some roots exhibit ortho-gravitropism and grow parallel to gravity. Others are diagravitropic (grow 90° from parallel), plagiogravitropic (~45° from parallel), or agravitropic (no response to gravity at all). All of these responses combine to direct the final three-dimensional shape of the overall root system.

10.5 The Root Rhizodermis Interacts Directly with the Soil

It should be noted that many authors use the term “epidermis” for the outermost layer of root tissues in the primary state of growth. However, it is more appropriate to utilize the term rhizodermis

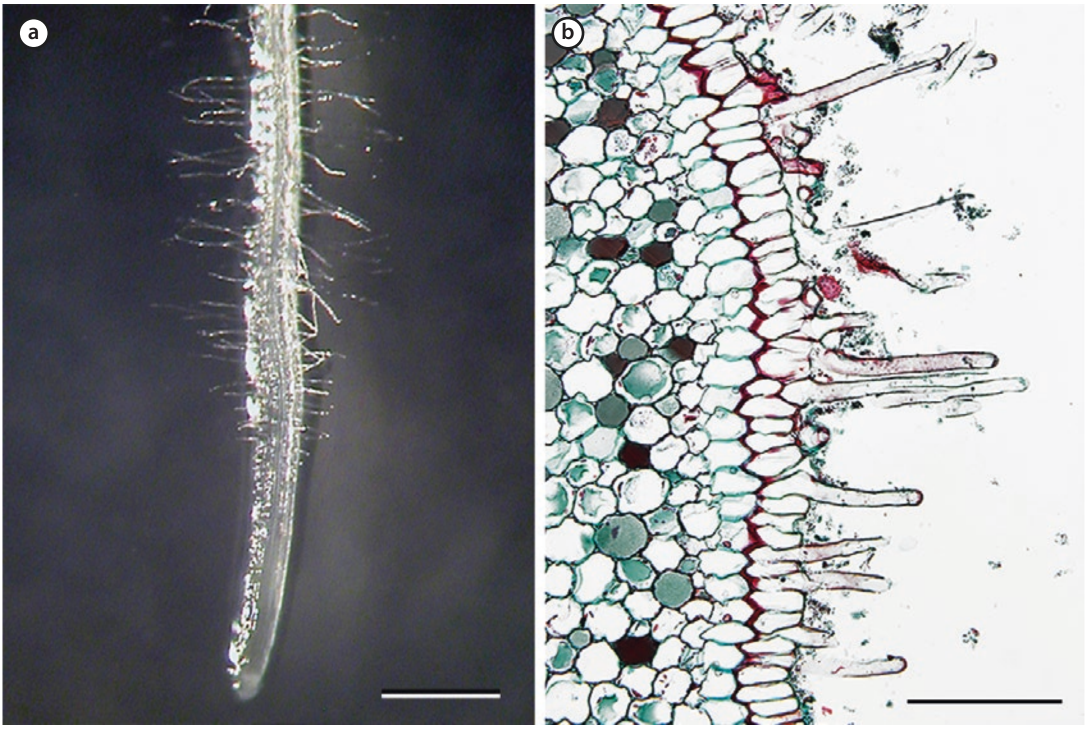


Fig. 10.5 **a** Root hairs on the primary root of the lyre-leaved cress (*Arabidopsis lyrata*). Note that root hairs are not found at the root tip; the hairless regions represent the zones of division and elongation. **b** Cross-section of an anthurium (*Anthurium* sp.) root showing root hairs. Scale bars = 200 µm in **a** and 100 µm in **b**. (**a**, **b** RR Wise)

(sometimes called the **epiblem**), since this tissue in root systems functions very differently from that of stems and leaves. In its underground state, the rhizodermis has no stomata, it is specialized for the absorbance of water and mineral substances, it produces mucigel as a lubricant, and it is never covered by a cuticle but develops short-living root hairs. Secondary development may lead to multiple layers and heavy sclerification. Because of these significant structural and functional differences with the epidermis of leaves and stems, the designation of "rhizodermis" will be employed in this text regarding root anatomy.

A rhizodermis differs from the root periderm in that the rhizodermis arises during primary growth from the protoderm, or from protoderm derivatives. The periderm arises from a phellogen that develops de novo in the root **pericycle**. Initiation and development of the root phellogen is discussed in ► Sect. 16.2.

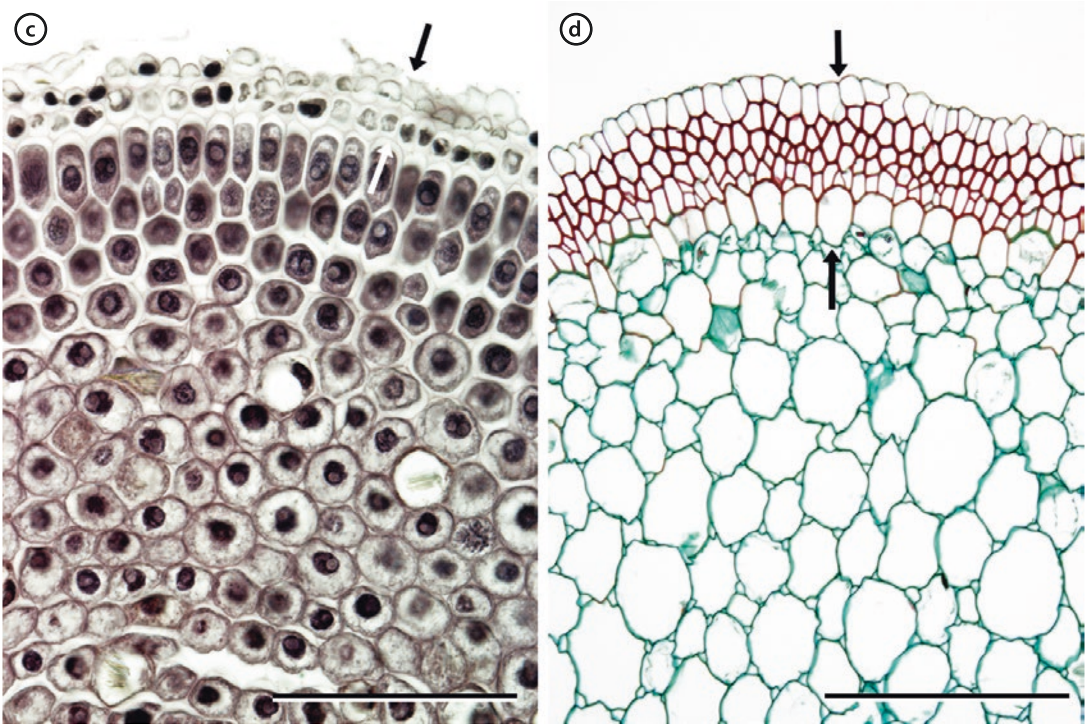
The rhizodermis in the primary state of growth is quite different anatomically from that in the secondary state of growth. Primary growth represents an opportunity for roots to increase in length in search of exploitable resources of water and minerals. Therefore, they are specialized for uptake with root hairs being a major route for the entry of water and minerals. Secondary growth involves strengthening the root to provide maximum anchorage.

Root hairs begin to develop near the root tip (◘ Fig. 10.5a, b) but only after that area of the root has achieved maximum elongation (refer to ► Sect. 10.3). They arise from rhizodermal cells positioned over the radial cell wall between cortical cells. The root hairs start from a protuberance at the apical end of elongate rhizodermal cells via tip growth (Ryan et al. 2001). For growth to occur, there is a demand for a rich Ca^{+2} gradient and dictyosome transport producing vesicles with newly formed cell wall materials to fuse with the cell membrane. Cells of the rhizodermis giving rise to root hairs are termed **trichoblasts**, whereas those that do not produce root hairs are designated as **atrichoblasts**. Most root hairs only survive for 1 or 2 days but by that time the root tip has elongated and new root hairs have developed (Grierson et al. 2014).

It is no coincidence that the zone of maturation, where root hairs develop, is also the area where the developing stele is the most permeable. Xylem, phloem, and the endodermis mature at this same level, giving the water and ions taken up by the root hairs a path of least resistance to the xylem transpirational stream.

Upon further development, multiple rhizodermal layers may arise, as is common in the irises (◘ Fig. 10.5c). The multiple layers are not a true periderm because they are the products of cell divisions in the rhizodermis, not in the phellogen (refer to ► Sect. 10.9).

Epiphytic orchids have a multilayered rhizodermis called the **velamen** (◘ Fig. 10.5d). A typical velamen has an outer layer of cells and an inner layer (or layers) of heavily sclerified cells, the



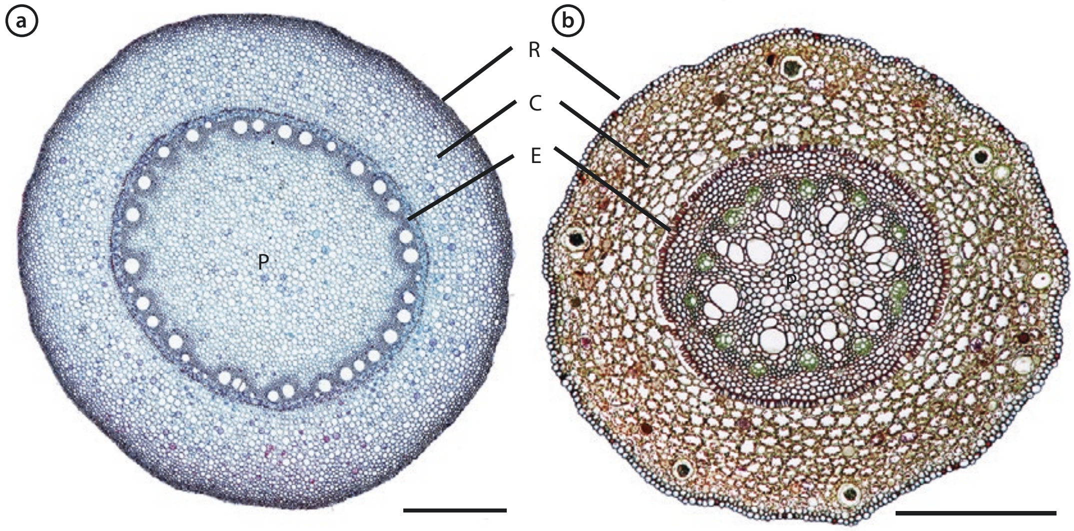
◘ **Fig. 10.5** **c** Iris (*Iris domestica*) roots have a multiple-layered rhizodermis, indicated as the region between the white and black arrows. **d** Aerial roots of orchids (unidentified species) have a velamen (layers of cells between the two black arrows). Note the lignified (stained red) cell walls of the inner layers of the exodermis. Scale bars = 50 µm in **c** and 100 µm in **d**. (**c**, **d** RR Wise)

exodermis (◘ Fig. 10.1c). The velamen serves to protect the root from transpirational loss as well as binding the root to the underlying substrate. In addition, it also absorbs atmospheric moisture and ions (Zotz and Winkler 2013) as well as providing a protection from harmful sunlight UV-B irradiation (Chomicki et al. 2014). The velamen arises from the root apex through a series of divisions that leave most of the cells dead upon maturity.

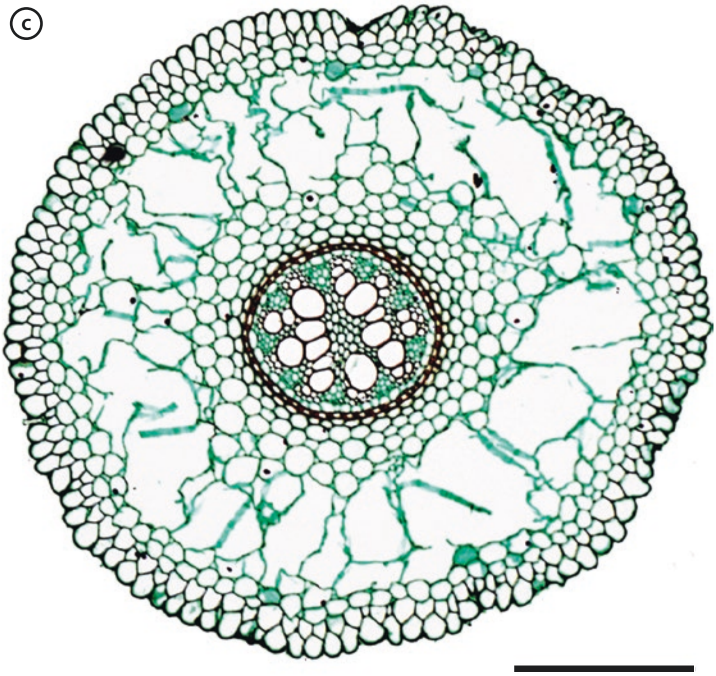
Monocot roots do not show secondary growth and therefore are incapable of periderm development. The outer layers of persistent roots may become thicken and become cutinized and lignified. Eudicot roots do show secondary growth (refer to ► Sect. 10.9) with perennial eudicots such as willow (*Salix* sp.) and pear (*Pyrus* sp.) generating a de novo phellogen that produces a bona fide periderm (refer to ► Chap. 16—Periderm).

10.6 The Root Cortex, Limited by the Endodermis, Is a Site of Storage and Oxygen Transport

The root cortex is parenchymatous tissue derived from the ground meristem. The root cortex, in keeping with its role in storage, is often much larger than the stem cortex. The cortex may become heavily sclerified in older monocot roots. It is bounded by rhizodermis or exodermis to the exterior and endodermis to the interior (◘ Fig. 10.6a, b). For many roots, it is the main site of starch storage, as can be seen in the *Ranunculus* roots shown in ◘ Fig. 10.7b, c. It may contain resin ducts, crystals, or other inclusions. Also, the cortex is the site of aerenchyma (◘ Fig. 10.6c) in those roots that function in gas exchange (◘ Fig. 10.1d).



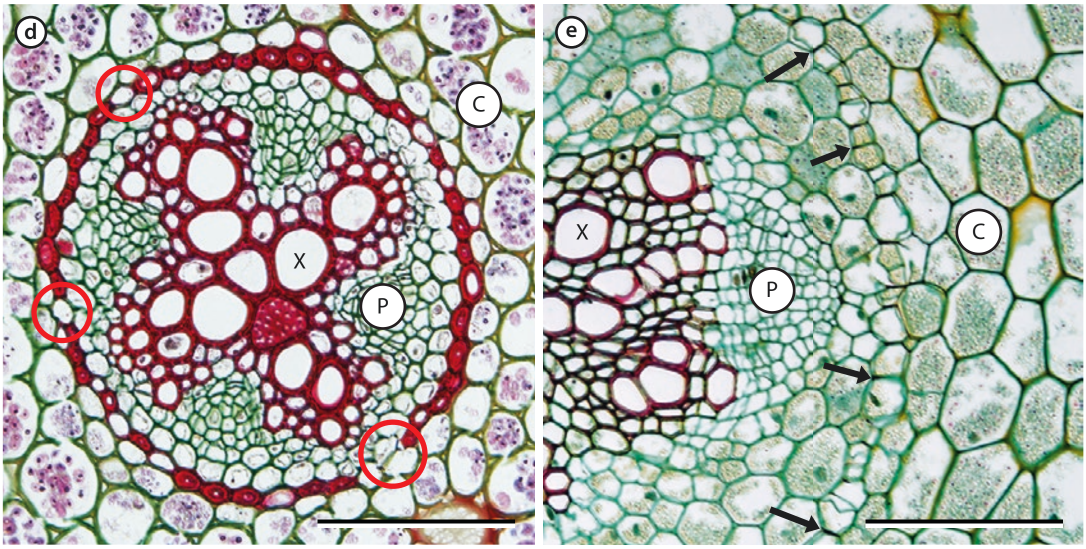
◘ **Fig. 10.6** **a**, **b** Cross-sections of **a** maize (*Zea mays*) root and **b** greenbrier (*Smilax* sp.) root. R, rhizodermis; C, cortex; E, endodermis; P, pith. Scale bars = 500 µm. (**a**, **b** RR Wise)



◼ **Fig. 10.6** **c** Aerenchyma in the cortex of lily (*Lilium michiganense*) root. Scale bar = 250 µm. (RR Wise)

The cortex is limited to the interior by the **endodermis**, a structure found in almost all roots, but much less so in stems (► Sect. 11.6). As described in ► Sect. 10.1, the endodermis is a single layer of cells that does not permit the free flow of water and ions between the individual cells but rather forces such materials to cross a cell membrane. This is due to presence of a Casparian strip (named for Johann Robert Caspary, a German botanist who lived from 1818–1887), which is a band of suberized lignin and proteins that covers the radial and transverse (anticlinal) walls of the endodermis. It is a component of the primary cell wall. Its presence forces the water and solutes to pass from the apoplast through the plasma membrane via a symplastic route to cross the endodermis. In monocots, the entire cell may develop thick deposits of suberin as the root matures. After entering the endodermal cells, the water can then move freely to the xylem where it is swept upward to the leaves in a stream of transpirational flow (refer to ► Sect. 10.1). **Passage cells** (sometimes called transfusion cells) lack the heavy suberization and provide for a diffusional pathway with less resistance. They tend to be located at the ends of the xylem poles (◼ Fig. 10.6d).

In most instances, xylem water is under tension (the opposite of pressure); water is pulled through a plant from the soil to the leaves by the evaporation or water from the leaves (transpiration is explained in ► Sect. 7.2). The root endodermis allows for the development of xylem pressure—called **root pressure**—the only instance in which xylem water is not under tension. Root pressure develops because the ions that are moved across the endodermis and loaded into the stele are osmolytes. That is, they bind water. This lowers the water potential of the xylem water and draws additional water into



◘ **Fig. 10.6** **d** The entire endodermis in buttercup (*Ranunculus acris*) is seen in this view as a dark red circle separating the cortex (C) to the outside from the phloem (P) and xylem (X) on the inside of the stele. The endodermis has heavily suberized cell walls. A Casparian strip is present but obscured by the lignin (stained red) in the thick cell walls. Three passage cells are indicated by the red circles at 5:00, 9:00, and 11:00. **e** A portion of the endodermis in baneberry (*Actaea spicata*) is shown at a higher magnification. The endodermal cell walls are not suberized, and the Casparian strip appears as dark bands on the anticlinal cell walls (arrows). The phloem (P) is to the outside of the xylem (X) indicating that it is a product of the vascular cambium (refer to ► Sect. 10.9). *Ranunculus* and *Actaea* are both in the Ranunculaceae. Scale bars = 50 µm in **d** and 100 µm in **e**. (**d**, **e** RR Wise)

the stele, generating a slight pressure. Root pressure is insufficient to push water more than a few centimeters up a stem; whereas xylem tension is capable of pulling water to the top of a 100-meter tree. As such, it plays little to no role in whole plant transpiration, unless the plant is very short. Root pressure is responsible for the phenomenon of **guttation**, the forcing of water out of leaf hydathodes (► Sect. 13.1.5). Guttation is most often seen early in the morning, before stomata have opened, and transpiration has the opportunity to develop a tension in the xylem.

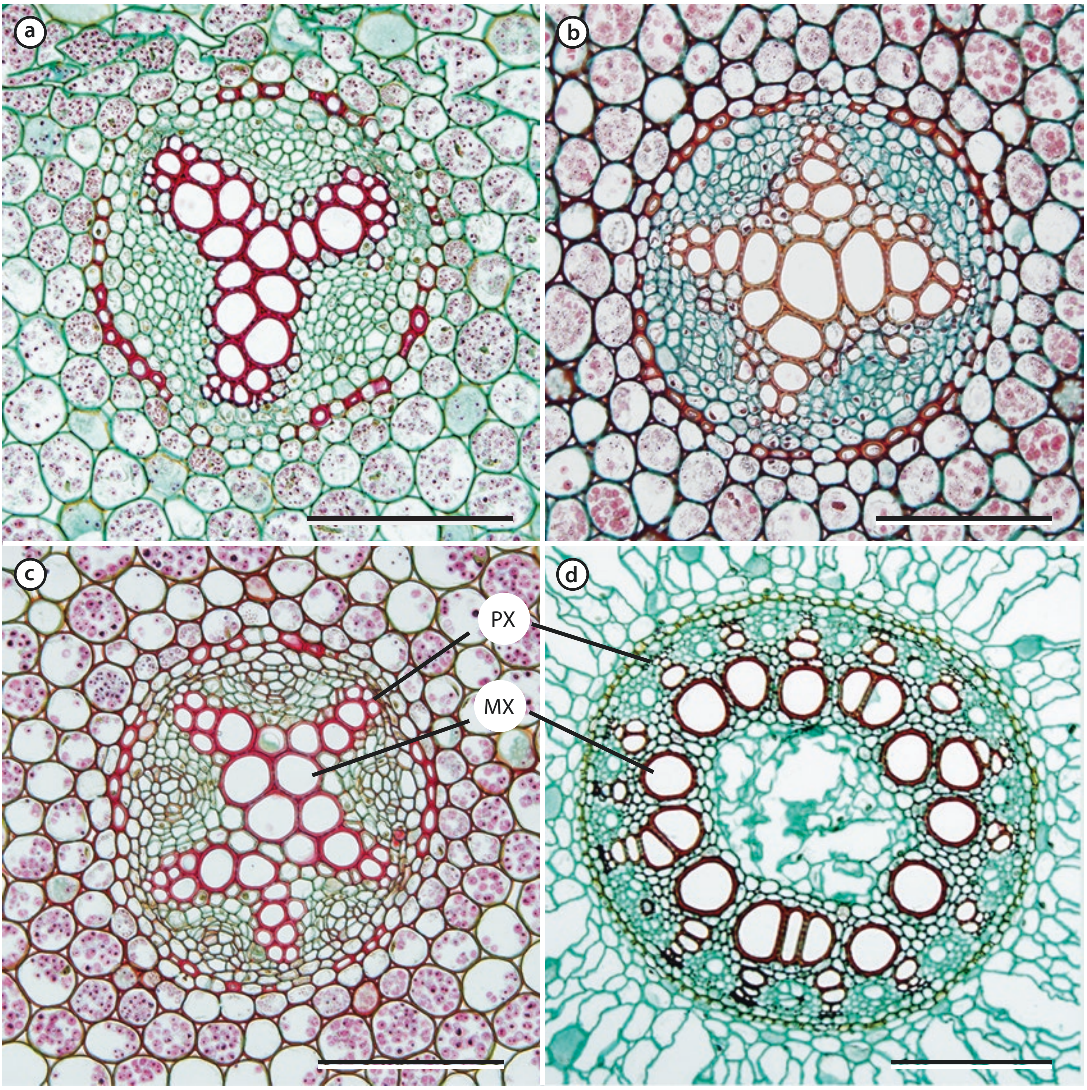
The exodermis lies between the rhizodermis and cortex. Not all roots have an exodermis; an example is shown in the orchid root in ◘ Fig. 10.5d. The exodermis is a functional equivalent of the endodermis. It may be suberized, cutinized, and contain Casparian strips on the anticlinal walls. Like with the endodermis, water and ions must pass into the symplast of the exodermis cells to enter the root cortex (◘ Fig. 10.6e).

10.7 The Stele Contains the Pericycle and the Xylem and Phloem of the Vasculature

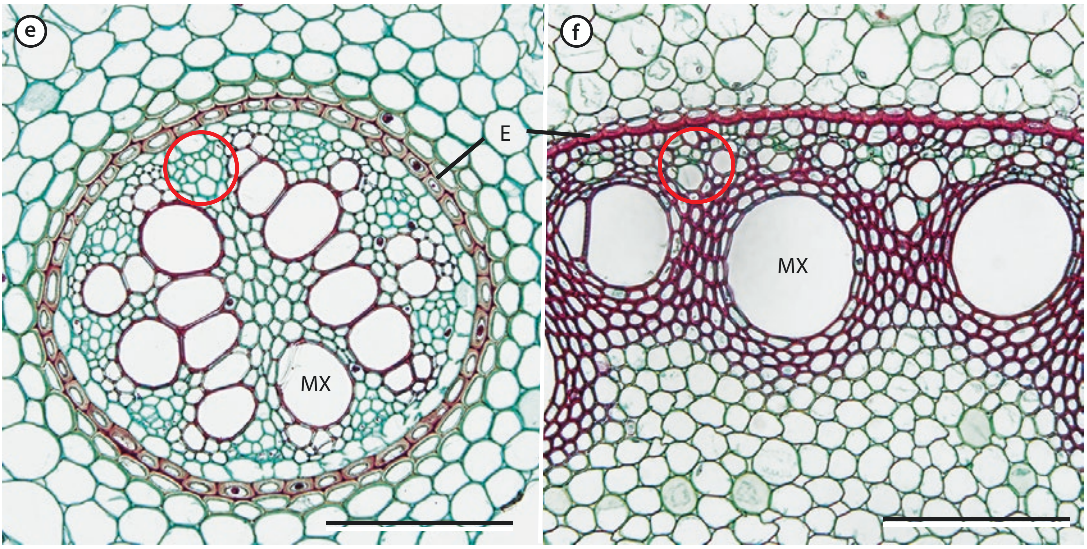
The central vascular cylinder of the root is called the stele, similar in concept to the stele found in many stems (refer to ► Chap. 11). The root stele is bound by the endodermis to the exterior and contains xylem, phloem, parenchyma (in some but not all cases), and a meristematic layer, the pericycle, which is the source of lateral roots.

Unlike stems in which the vascular tissues are arranged in discrete bundles of xylem and phloem and spread throughout the stem, all of the root vasculature is a more or less solid cylinder of xylem in the middle with phloem to the exterior. Thus, most eudicot and monocot steles are protosteles. Pith is rare in eudicots as it gets crushed early on in root development but somewhat common in monocots (refer back to ◘ Fig. 10.6a, b).

Root xylem is arranged in a spoke-like pattern with the number of spokes, or "xylem poles," being characteristic of the taxon. Eudicots typically have discrete xylem poles. A two-arm pattern is called **diarch**, followed by **triarch**, **tetrarch**, **pentarch**, and up to as many as eight poles (◘ Fig. 10.7a–c). Monocots are typically **polyarch** with numerous xylem poles arranged in a more or less ring



◘ **Fig. 10.7** **a**–**d** Images of **a** a triarch stele in a buttercup (*Ranunculus acris*) root, **b** tetrarch buttercup stele, **c** pentarch buttercup stele, and **d** polyarch asparagus (*Asparagus officinalis*) stele with multiple individual groupings of xylem. PX, protoxylem; MX, metaxylem. Scale bars = 100 µm in all panels. (**a**–**d** RR Wise)



◘ **Fig. 10.7** **e** Stele in a lily (*Lilium michiganense*) with nine patches of phloem (one is circled) in between metaxylem (MX) groupings. **f** Edge of the stele in a maize (*Zea mays*) root showing the scattered nature of the phloem to the exterior of the metaxylem (MX). Scale bars = 100 µm in both panels. (**e**, **f** RR Wise)

shape at the periphery of the stele and a central pith (◘ Fig. 10.7d). Larger monocot roots have a polyarch with so many xylem poles that they may be called an atactostele (for "scattered" xylem).

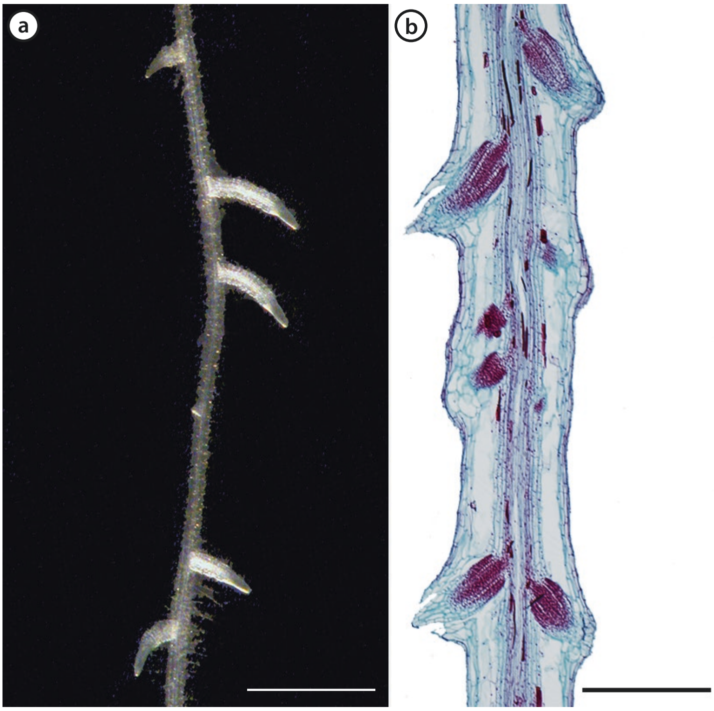
Monocot and eudicot roots both have an exarch pattern of vascular development with protoxylem to the exterior and metaxylem to the interior (◘ Fig. 10.7c, d). [Note that stem vascular development is endarch, ► Chap. 11].

In terms of phloem distribution, primary phloem in eudicot roots is positioned between the xylem arms, as seen in *Ranunculus* (refer back to ◘ Fig. 10.6d). Monocot distribution is similar but the polystelic nature of monocot roots results in individual groupings of xylem with phloem arranged in patches in between the groupings or scattered to the outside of the xylem (◘ Fig. 10.7e, f).

The pericycle is a single layer of parenchyma cells lying just inside the endodermis in all roots. They are prominent and can be seen in most of the figures in this section. Pericycle cells are meristematic and the source of all lateral roots (refer to ► Sect. 10.8). They also contribute to the vascular cambium and cork cambium in those roots that exhibit secondary growth (► Sect. 10.9).

10.8 Lateral Roots Originate in the Pericycle and Push Through the Cortex

Lateral (or **branch**) roots develop off of an existing root, starting just behind the zone where root hairs senesce (◘ Fig. 10.8a, b). In terms of length, quantity, and volume, they represent the vast majority of roots in a root system. Primary laterals arise from a taproot, secondary laterals arise from primary, tertiary from a secondary, and so on. In contrast to the shoot where branches originate



■ **Fig. 10.8** **a** Lateral roots arising from the primary root of a lyre-leaved cress (*Arabidopsis lyrata*) seedling. Although the root caps cannot be seen at this magnification, the root tips are bending down, indicating that functional root caps are present on all of the developing lateral roots. **b** Longitudinal section of a black willow (*Salix nigra*) root. Each of the red protrusions is a developing lateral root. Scale bars = 2 mm in **a** and 250 µm in **b**. (**a**, **b** RR Wise)

exogenously from the apical meristem, lateral (or branch) roots are initiated **endogenously** in the pericycle without any relation to the apical meristem (■ Fig. 10.8c–g).

Typically, the point of origin of a lateral root is opposite to the xylem in eudicots and opposite to the phloem in monocots. Here, the pericyclic cells become densely cytoplasmic and resume meristematic activity. This growth occurs through repeated periclinal cell divisions from a few cells designated as founder cells (■ Fig. 10.8h). The lateral root primordial growth must penetrate the endodermis, cortex, exodermis, and the rhizodermis in order to appear on the surface of parental root. These tissues are stretched and finally ruptured (■ Fig. 10.8d–f). A root cap meristem develops when root tip is about halfway through the cortex (■ Fig. 10.8i) and is well defined by the time the root emerges. The exit hole causes damage that is sealed off with a special corky layer surrounding the new lateral root (■ Fig. 10.8j). Cells of the emerging lateral root develop into xylem and phloem and connect to the vasculature in the stele of the parent root.

The reason for the inability of the root apical meristem to produce lateral roots, and for that function to occur further back in the root via the pericycle, no doubt has to do with the nature of the substrate through which roots grow. Shoots can generate both primary growth and new organs at the shoot tip because they grow through air. There is no resistance to growth. Root tips, on the other

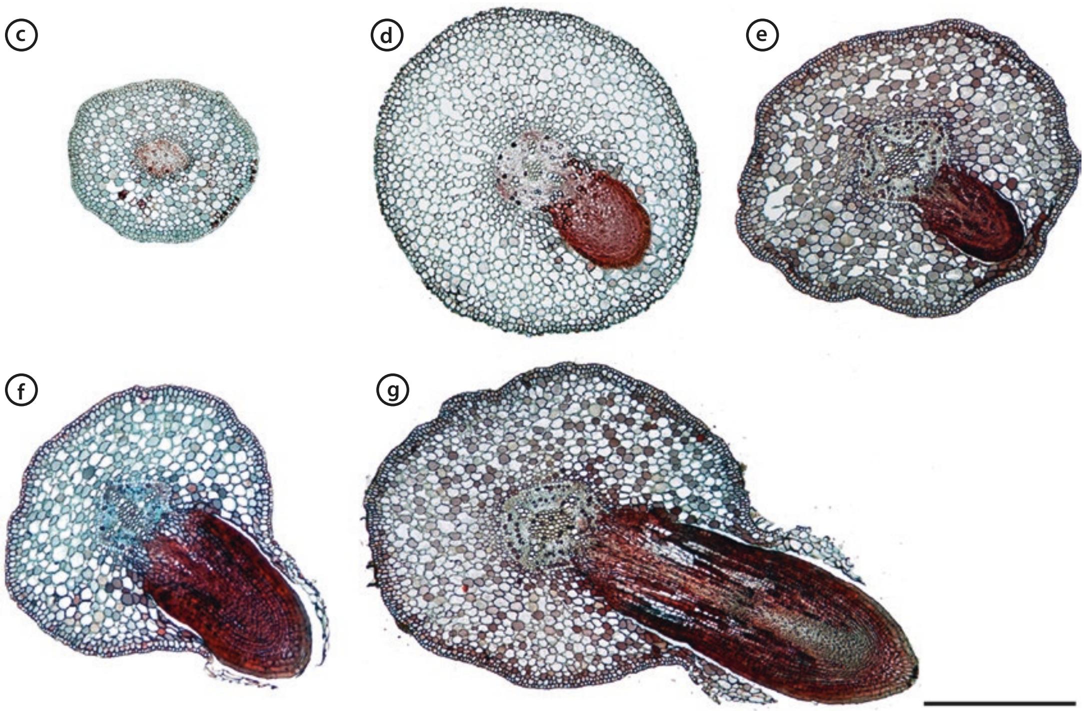


Fig. 10.8 **c**–**g** A sequence of light micrographs of willow (*Salix* sp.) lateral roots arising from the central vascular stele. Scale bar = 0.5 mm. (**c**–**g** RR Wise)

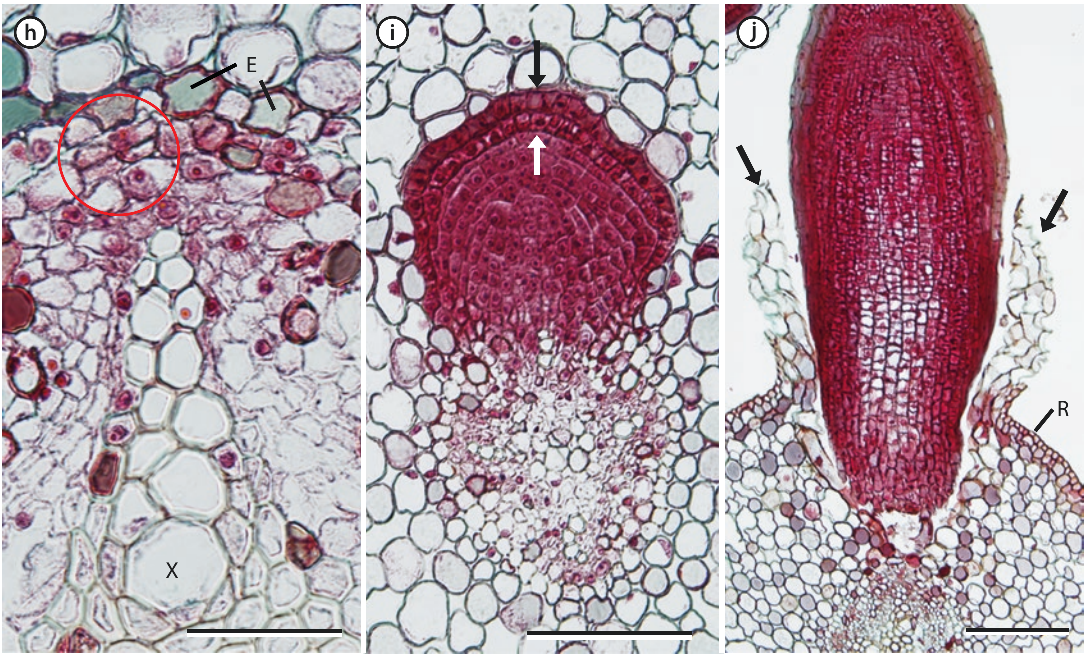


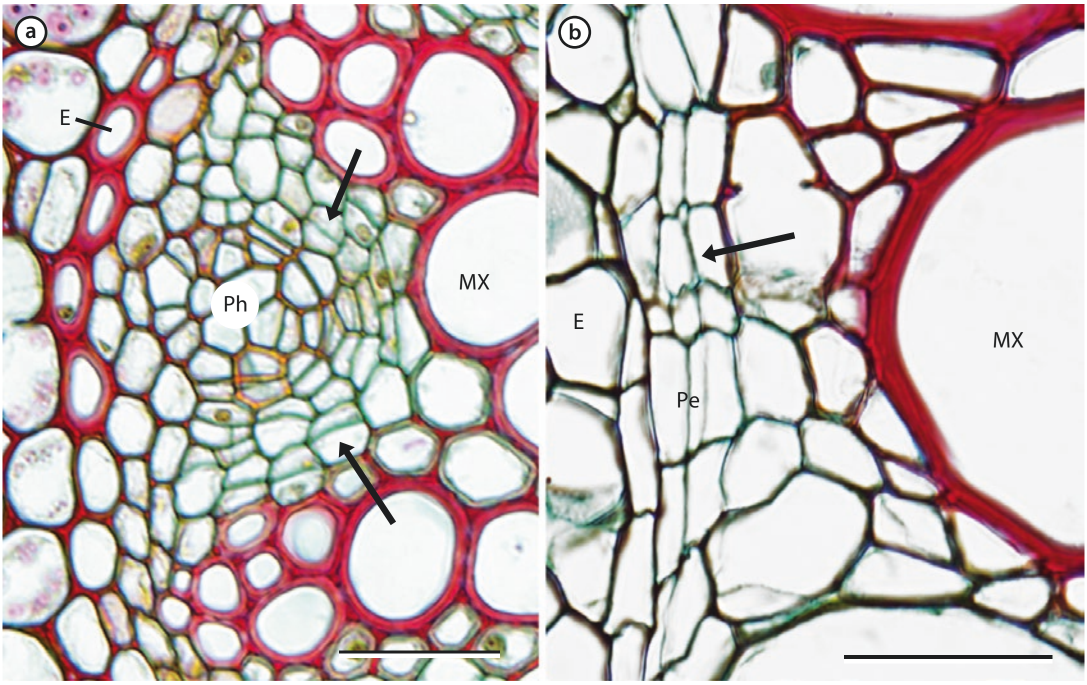
Fig. 10.8 **h**–**j** Root development in black willow (*Salix nigra*). **h** Very early stage in lateral root development. Two pericycle cells (in red circle) opposite the xylem (X) arm are dividing in a periclinal plane. The endodermis (E) lies to the outside of the pericycle. **i** At a later stage, the root tip is about halfway through the cortex and has developed a root cap two cell layers thick (between arrows). **j** After pushing through the rhizodermis (R), the hole in the parent root is sealed by a collar of corky cells (arrows). Scale bars = 25 μm in **h**, 50 μm in **i,** and 100 μm in **j**. (**h**–**j** RR Wise)

hand, have to push through soil as they engage in primary growth (i.e., elongate). If lateral roots were produced at the root apex, they would be torn off as the tip pushed through the soil. Lateral roots are initiated further back on the developing root, in a region that is no longer undergoing elongation.

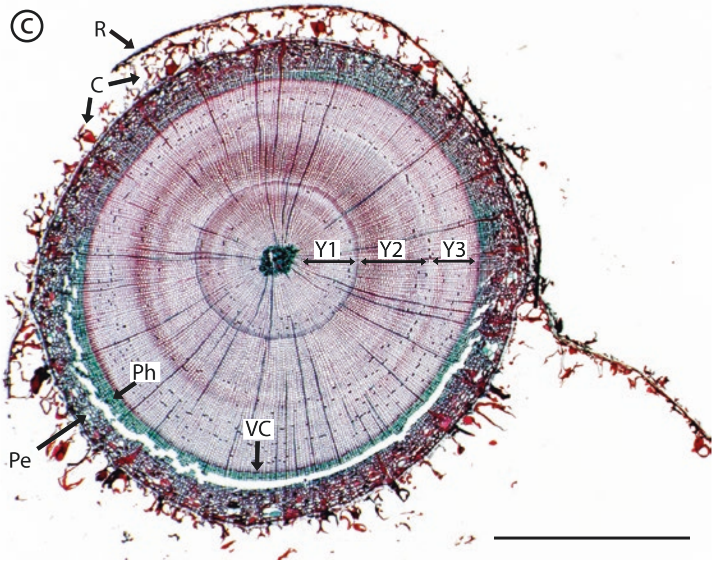
10.9 The Transition from Primary to Secondary Growth in Roots Involves the Development of Two New Meristems

The roots of gymnosperms and woody eudicots exhibit secondary growth. Doing so requires the development of two meristems—a vascular cambium (to produce secondary xylem and phloem) and a phellogen (to replace the rhizodermis with a corky periderm)—both of which must form a continuous cylinder or meristematic tissue. The phloem and the pericycle play roles in the origin of these secondary meristems.

The first step is the differentiation of phloem cells at the inner edge of the protophloem strands into **cambial initials** capable of generating xylem to the inside and phloem to the outside (◘ Fig. 10.9a). Subsequently, pericycle cells to the exterior of the protoxylem poles also divide to produce more new cells of the vascular cambium (◘ Fig. 10.9b). Eventually, the two groups of dividing cells will merge to form a circular meristem and complete an encompassment of the primary xylem.



◘ **Fig. 10.9** **a** Phloem (Ph) cells in a buttercup (*Ranunculus acris*) root exhibiting meristematic activity by dividing in a periclinal plane (arrows). The phloem sits between two metaxylem (MX) arms and is bounded by the endodermis (E) to the exterior. **b** Pericycle (Pe) cells dividing in a periclinal plane (arrow) and contributing to the vascular cambium in a potato (*Solanum tuberosum*) root. Endodermis (E) is to the exterior and metaxylem (MX) to the interior. The cortex is to the left in both images. Scale bars = 25 µm in both panels. (**a**, **b** RR Wise)



◻ **Fig. 10.9** **c** A cross-section of a woody gymnosperm (*Metasequoia glyptostroboides*) root showing a central decomposed pith region of the primary growth and 3 years of secondary growth (Y1, Y2, Y3) with wood rays extending in all directions. Just outside a layer of vascular cambium (VC) is the living secondary phloem (Ph, stained green), and to the outside there is a well-developed periderm (Pe). The original cortex (C) and rhizodermis (R) are in the process of shedding. Scale bar = 1 mm. (RR Wise)

The vascular cambium arises from the inner cells of this new meristem, while the phellogen arises from the outer cells. A periderm consisting of cork toward the outer surface and phellogen (cork cambium) toward the inner surface develops. Both the vascular cambium and the phellogen divide periclinally (as a new wall is formed parallel to the root surface) and anticlinally (with a new wall developing perpendicular to the root surface) which together produce cells that form the thickened root. Note that as in the case of stems (refer to ► Chap. 11), secondary growth is not found in monocots or herbaceous eudicots.

All of the tissues outside of the pericycle, which include the rhizodermis, exodermis, cortex, and endodermis, eventually die and are shed (◻ Fig. 10.9c). The pericycle-derived phellogen generates the periderm for the remaining life of the root. As the vascular cambium becomes active at the start of each growing season, the production of new xylem and phloem increases the girth of the root. With multiple layers of xylem, the root may also become woody and reveal growth rings as in stem wood.

10.10 Symbioses Between Roots/Bacteria and Roots/Fungi Greatly Enhance Nutrient Acquisition

Nitrogen is one of the most essential elements for life as it is a component of nucleic acids, proteins, amines, and a variety of other compounds. Many of these are not only required for the plant, but for other forms of life, as well as in commercial products. While nitrogen makes up 80% our atmosphere, it is not readily available for uptake and use by most organisms since it exists as an essentially inert gas (N_2) due to a triple covalent bond between two nitrogen atoms. In order for N_2 to be made available to organisms, it must be chemically reduced and combined in the form of ammonium (NH_4) in a process called nitrogen fixation.

The electrical energy of lightning produces a small amount of nitrogen fixation in the atmosphere via physical nitrogen fixation (PNF). Biological nitrogen fixation (BNF) is carried out by living organisms, all of them prokaryotic. A few of the BNF bacterial taxa are free-living; however, the largest flux of bioavailable nitrogen into the ecosystem comes from bacteria that form a symbiotic association with plants. In brief, the following reaction represents a summary of the process:

$$\mathrm{N_2 + 8H^+ + 8e^- + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16Pi}$$

where N_2 = nitrogen gas, H^+ = hydrogen ions, e^- = electron, ATP = adenosine triphosphate, NH_3 = ammonia, H_2 = hydrogen gas, ADP = adenosine diphosphate, and Pi = inorganic phosphate. Nitrogenase is the enzyme responsible for catalyzing this reaction.

Although BNF symbioses can be found across the kingdom Plantae, including some tropical grasses (*Azosprillium*) and the aquatic fern *Azolla*, the majority, and the best studied, are in association with members of the family Leguminosae and involve species of *Rhizobium* bacteria. The bacterium receives carbohydrates from the plant, and the host plant obtains nitrogen in a bioavailable form from the bacteria.

Rhizobium bacteria are found free-living in the soil, but they must infect a plant root to be capable of nitrogen fixation. Roots release molecules into the rhizosphere that attract the bacteria (homoserine, in the case of *Pisum sativum*). Bacteria are attracted to the signal and move toward the root (positive chemotaxis). Bacteria accumulate in the rhizosphere and multiply. Bacteria release “nod factors” (small polymers of chitin derivatives) that stimulate root hair production. The bacteria release mitogenic signals that stimulate cytokinin production and initiate the formation of a meristem in the cortex of the root, called the primary nodule meristem. The root pericycle becomes active and grows outward, eventually fusing the root vasculature with that of the nodule. Bacteria penetrate the wall of the root hair by secreting pectinase, cellulases, and hemicellulases and grow an “infection thread” through the root hair toward the developing nodule in the root cortex. Growth of the primary nodule meristem pushes the entire mass out of the root to form a large nodule (◘ Fig. 10.10a) filled with bacteria (◘ Fig. 10.10b). The bacteria are “released” into the symplast of the plant cortical cells by budding off of infection thread but never technically enter the cytoplasm. The cells are surrounded by a bit of the infection thread membrane that further thickens by the inclusion of polysaccharides from the host plant into a “peribacteroid membrane” (◘ Fig. 10.10c). The vasculature of the host plant grows to and supplies the nodule with xylem and phloem.

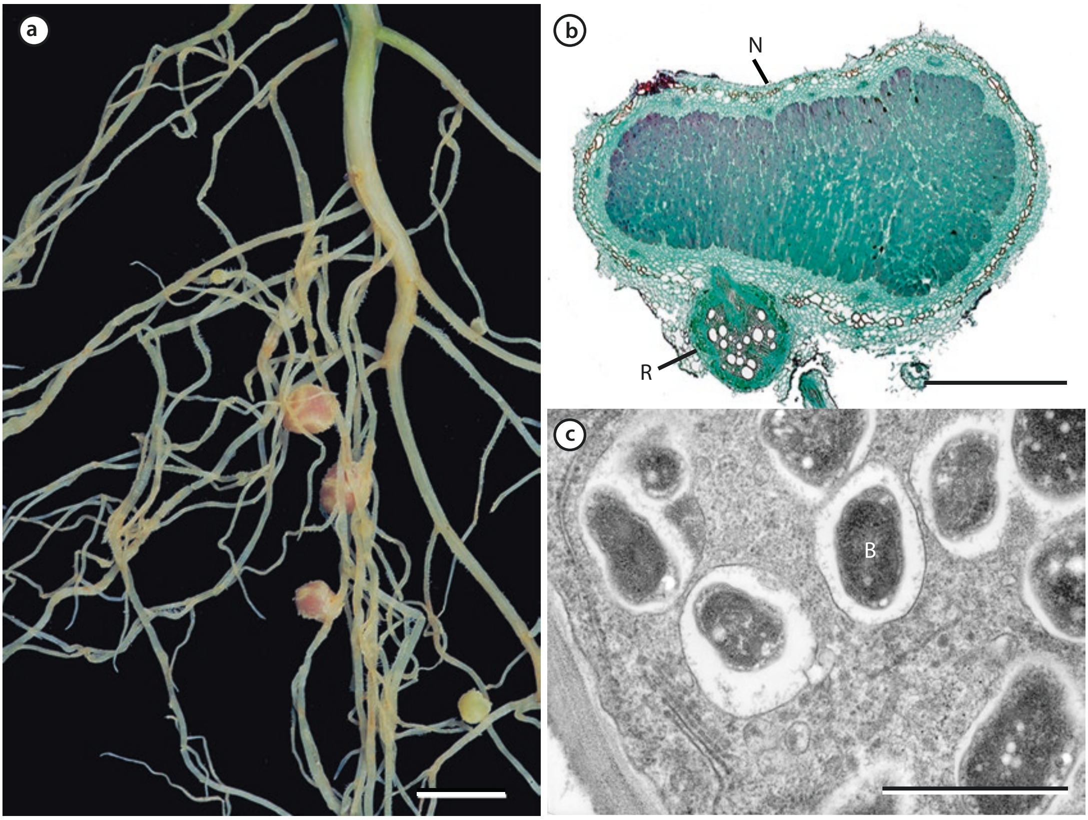


Fig. 10.10 a–c Root nodules. **a** *Robinia pseudoacacia*. Note red leghemoglobin in the nodules. **b** Soybean (*Glycine max*) root nodule. R, root; N, nodule. **c** TEM of bacteroides (B) in a soybean nodule. Scale bars = 1 cm in **a**, 500 μm in **b,** and 1 μm in **c.** (**a**, **b** RR Wise; **c** L Howard, Dartmouth Electron Microscope Facility, public domain)

Nitrogen fixation usually begins around 10–14 days after the nodules have formed and is mediated by a multienzyme complex called nitrogenase. The energy (in the form of 16 ATP per N_2 fixed) is supplied by plant mitochondria using carbohydrates supplied by the phloem. Nitrogenase is exquisitely sensitive to oxygen. Therefore, the plant synthesizes a red, heme-containing, oxygen-binding protein called leghemoglobin. It is responsible for the pinkish color of the nodules seen in ◘ Fig. 10.10a and reduces the oxygen levels within the nodule. Mitochondria can operate at O_2 levels too low to inhibit nitrogenase, so the respiratory supply of ATP is maintained. The NH_3 (ammonia) formed by nitrogenase is toxic. It is converted to amine groups which are used immediately in the synthesis of glutamate, glutamine, or a variety of transportable amino acids (this takes place in the nodule proplastids, refer to ► Sect. 3.5.1). The amino acids are loaded into the xylem and transported throughout the plant via the transpiration stream.

A second form of symbiotic relationship exists between plant roots and fungi. The vast majority of plants—perhaps up to 80%—form symbiotic associations with fungi that provide them with better access to soil nutrients while also providing a defense of diseases and toxic substances (Ercolin and Reinhardt 2011). Such an association is termed mycorrhization (myco, fungus; rhiza, root). It is of benefit to both partners because the plant obtains phosphates and other minerals while simultaneously providing the fungus with sugars and other organic foods. Plants that benefit the most from mycorrhizal associations are those which grow on nutrient-poor soils. The fungi indirectly increase the active surface and absorbent area of the root since the symbiotic fungi effectively spread further through the soil. Additionally, many of the mycorrhizal fungi not only form a physical barrier to the presence of pathogens but also may provide antibiotic compounds against them.

There are two basic forms of mycorrhizae: ectomycorrhizae and endomycorrhizae. Ectomycorrhizal fungi ("outside" root fungus, EMF) infection initiates the formation of short roots that are specialized in nutrient uptake (◘ Fig. 10.10d, Martin et al. 2016) and form a covering of hyphae on the outside of those roots called a mantle (◘ Fig. 10.10e). They also penetrate the root tissue and grow through the apoplastic (cell wall) spaces inside the cortex, forming a structure called the **Hartig net** (◘ Fig. 10.10f). While the fungus is indeed inside the root, it only grows in the cell wall space and does not penetrate into the cells (◘ Fig. 10.8d, e). Thus, the "ecto" (outside) prefix technically applies, even though the fungus is inside the root.

◘ **Fig. 10.10** **d** Ectomycorrhizae on the surface of a blue spruce (*Picea pungens*) root. Note the cluster of short lateral roots (arrow) covered by a thick mantle of light-brown fungus. The lateral root to the top is not heavily infected. Scale bar = 1 mm. (RR Wise)

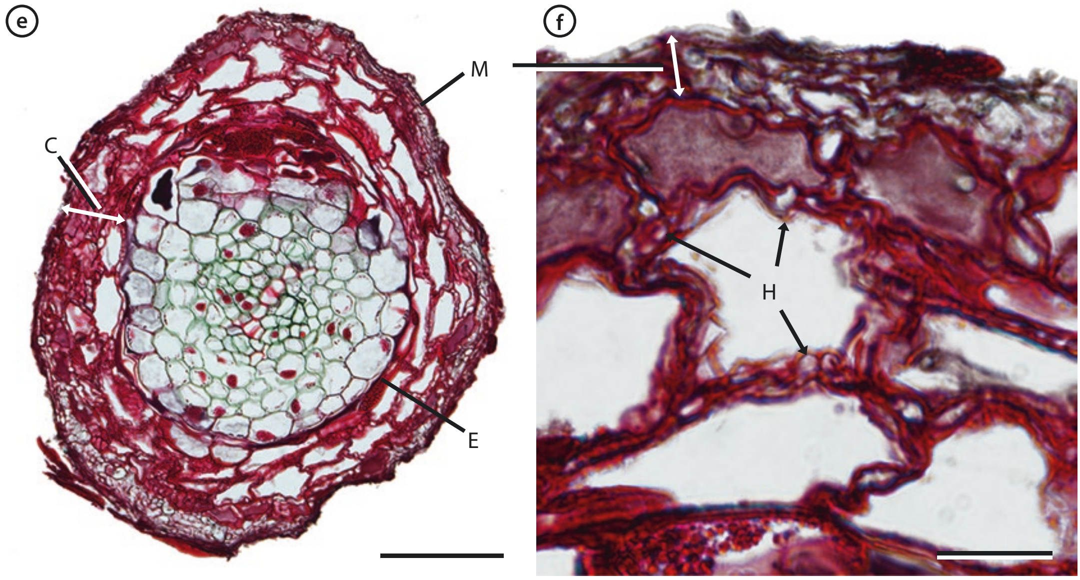


Fig. 10.10 e, f Mantle and Hartig net in a pine (*Pinus* sp.) root. **e** The mantle (M) is a thin layer on the root surface. Then entire root cortex (C) is infected with the fungal hyphae of the Hartig net (stained red), but the fungus does not cross the endodermis (E) and enter the stele. **f** The individual hyphal cells (H) of the Hartig net can be seen occupying the apoplast of the cortical parenchyma cells. Scale bars =50 µm in **e** and 10 µm in **f**. (**e**, **f** RR Wise)

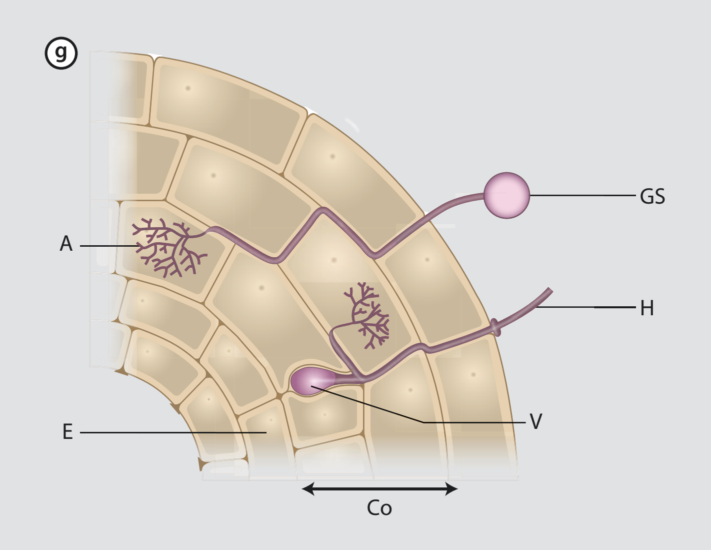


Fig. 10.10 g Drawing of an endomycorrhizal infection. A = arbuscule, Co = cortex, E = endodermis, GS = germinating spore, H = hypha, V = vesicle. (Modified from M. Piepenbring, CC BY-SA)

Endomycorrhizal fungi, on the other hand, grow into and penetrate individual root cells (◘ Fig. 10.10g). Once there, the hyphae form hyphal vesicles or a branched structure called an arbuscule (from “arbor” or tree); therefore, endomycorrhizal fungi of this type are also called arbuscular mycorrhizal fungi (AMF). AMF are far more widespread than EMF. It should be recognized that although the VA hyphae penetrate the interior space of the cells, they do not penetrate the plasma membrane and enter the symplast. The "endo" prefix was applied by light microscopists because the arbuscules occupy the cell interior. The advent of electron microscopy allowed plant scientists to see that the fungus does not truly enter the cell protoplast, but the "endo" (inside) prefix prevails. Mineral ions, primarily phosphate, are concentrated in the arbuscule, which only is present for a short time, perhaps 3–8 days. The arbuscule develops, matures, accumulates minerals, and is then absorbed by the host. Subsequent arbuscules may form in the same cell.

Box 10.2 An Ancient Symbiosis Within a Symbiosis Involving Transkingdom Gene Transfer

Arbuscular mycorrhizal fungi (AMF) infect the roots of host plants in a symbiotic relationship. The fungal partner (a member of the Kingdom Fungi) receives photosynthate from the host plant (Kingdom Plantae), and the host receives soil nutrients from the fungus. Curiously, there are numerous reports of a symbiotic bacterium (*Mollicutes*-related endobacteria or MRE—Kingdom Eubacteria) being hosted within the cytoplasm of some endomycorrhizal fungi, making for a three-partner, three-kingdom symbiosis. Torres-Cortés et al. (2015) further investigated this relationship by performing a genome analysis of an MRE hosted by *Dentiscutata heterogama*, a common AMF. The bacterial partner has a greatly reduced metabolic activity, as evidenced by a paucity of genes for energy production and conversion, carbohydrate transport and metabolism, and inorganic ion transport and metabolism. Several bacterial genes show similarity to genes found in a known AMF genome, and a very large group of bacterial genes have eukaryotic-like domains that are likely to serve regulatory functions within the eukaryotic host. Both observations strongly suggest horizontal gene transfer from the fungus to the bacterium and the ability of the bacterium to directly influence fungal physiology. This fungal/bacterial symbiotic relationship, and its somewhat novel transkingdom gene transfer, is an ancient partnership, perhaps as much as 400 million years old.

Reference: Torres-Cortés et al. (2015).

10.11 Chapter Review

Concept Review

10.1. *Roots and root systems serve multiple purposes.* Roots function in water and mineral ion uptake, anchorage, storage, and as the source of hormones that play key roles in root-to-shoot communication. The pathway for water and ions can take an apoplastic or a symplastic route to the stele. The endodermis directs the movement of ions from the apoplast into the symplast.

10.2. *Root system morphology is diverse and adapts to soil conditions* via *compensatory growth.* Eudicots have a taproot system, while gymnosperms and monocots have a fibrous root system. Lateral roots arise from the primary taproot. The primary root system of monocots is replaced by a secondary root system of adventitious, proper roots. Root growth responds to local soil conditions via compensatory growth to maximize access to water and minerals and avoid salinity, drought, and flooding.

10.3. *Primary growth of roots involves formation of tissues and their organization.* The root tip is covered by a protective root cap. The slimy mucigel it secretes and the cells it sheds lubricate and ease the passage of the root through the abrasive soil. The zone of division is the source of new cells. The zone of elongation pushes the root forward. Cells differentiate into their mature state in the zone of maturation.

10.4. *The root tip and root cap control the rate and direction of root growth.* The columella of the root cap senses gravity by the action of amyloplasts (statoliths) that settle in response to the gravitational field. This movement initiates growth responses that direct to elongate in a specific direction, usually, but not always, down.

10.5. *The root rhizodermis interacts directly with the soil.* The rhizodermis must be permeable to water and ions, resist microbial infection and help anchor the root in the soil. Root hairs are transient extensions of rhizodermal cells that greatly increase the surface area for water and ion uptake. Aerial roots produce a velamen to protect the root tip from desiccation and take up water and minerals.

10.6. *The root cortex, limited by the endodermis, is the site of storage and oxygen transport.* The root cortex lies between the rhizodermis and the endodermis and is used for storage and for providing a route for oxygen diffusion in flooded roots. The endodermis is an apoplastic barrier to the movement of water and ions from the cortex into the stele and is characterized by the presence of a Casparian strip in the radial cell walls. Root pressure develops inside the endodermis as a consequence of ion (and water) uptake by the xylem. The stele may be defined at the outer boundary by an exodermis, which lies just underneath the external rhizodermis. Some roots develop a polyderm, a multilayer of cells that develops internal to the endodermis and ultimately replaces the rhizodermis.

10.7. *The stele contains the xylem and phloem of the vasculature and the pericycle.* The eudicot stele has a star-shaped central core of xylem surrounded to the exterior by phloem in discrete patches. The xylem core may have two to eight arms or poles with the patterns named after the number of poles (diarch, triarch, tetrarch, pentarch). Monocots have numerous xylem poles and are termed polyarch. Patches of phloem are positioned between, and to the outside of, the xylem arms. The pericycle is the outer layer of the stele and is responsible for lateral root formation.

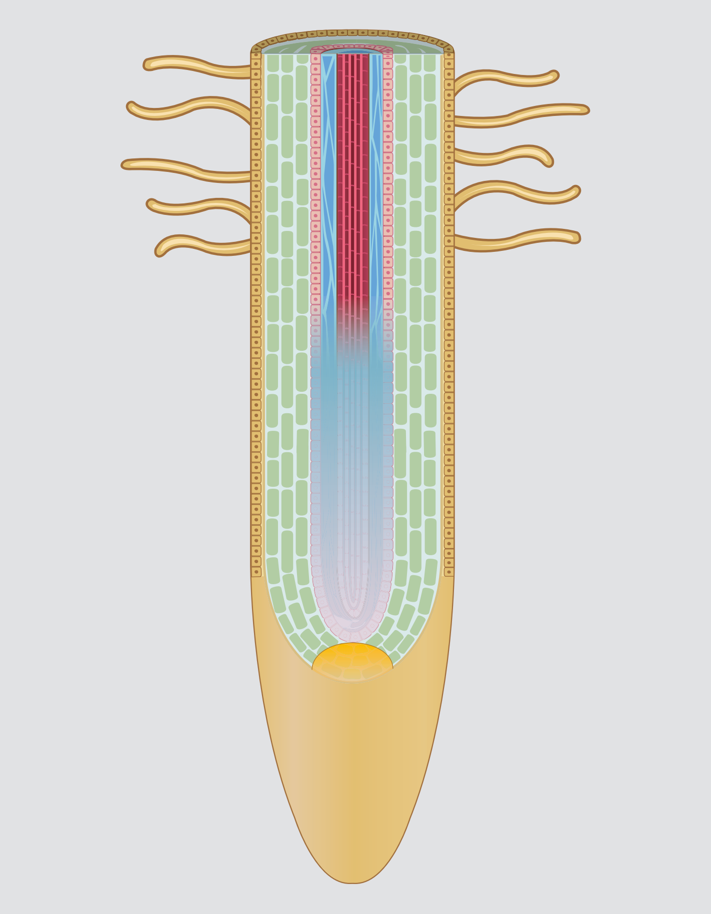
10.8. *Lateral roots originate in the pericycle and push through the cortex.* Lateral roots develop from existing roots. Lateral root development starts with meristematic divisions of pericycle cells and proceeds by pushing the developing root through the endodermis, cortex, and rhizodermis. The emergent lateral root has a fully developed root cap and is connected to the vasculature of the parent root.

10.9. *The transition from primary to secondary growth in roots involves the development of two new meristems.* In the transition from primary to secondary growth, cells to the interior of the phloem strands and exterior to the xylem poles become meristematic and produce a circular ring of diving cells in the root. Those cells to the interior of that ring mature into a vascular cambium which produces xylem and phloem. Those cells to the exterior of that ring mature into a phellogen, which produces the periderm. The original cortex and rhizodermis, which sit outside the new periderm, are shed.

10.10. *Symbioses between roots/bacteria and roots/fungi greatly enhance nutrient acquisition.* Plant roots have two major symbiotic relationships that greatly increase their ability of their root systems to access mineral resources—nitrogen-fixing bacteria and mycorrhizal fungi. In biological nitrogen fixation (BNF), bacteria capable of reducing gaseous nitrogen to the level of ammonia infect the roots of host plants, via root hairs. The host responds by initiating meristematic growth in the pericycle and the cortex. The large nodule that is produced is colonized by thousands of bacterial cells that engage in BNF. The host plant provides the carbohydrates needed by the bacteria, and the bacteria provide the host with reduced (bioavailable) nitrogen. Mycorrhizal fungi also infect plant roots. Ectomycorrhizal fungi cover the outside of the root and grow between the cells of the cortex. Endomycorrhizal hyphae penetrate the root cortical cells and develop tree-shaped arbuscules in which they accumulate minerals, mostly phosphorous. The arbuscules are short-lived, and the minerals they contain are absorbed by the host plant.

Concept Connections

? 1. On the figure below, label the root cap, three zones of differentiation, four meristems, and six mature tissues. Which of the mature tissues do each of the meristems give rise to?



Concept Assessment

2. The exodermis is derived from cells of the
   - a. rhizodermis.
   - b. cortex.
   - c. endodermis.
   - d. pericycle.
   - e. cambium.

3. The ability of roots to adjust growth to local soil conditions is called
   - a. positive gravitropism.
   - b. directional growth.
   - c. trichoblast formation.
   - d. compensatory growth.
   - e. meristematic adjustment.

4. Dicot roots typically do not possess
   - a. cortex.
   - b. rhizodermis.
   - c. pith.
   - d. endodermis.
   - e. pericycle.

5. Passage cells are found in which tissue?
   - a. metaxylem.
   - b. rhizodermis.
   - c. endodermis.
   - d. cortex.
   - e. pericycle.

6. In eudicots, lateral roots typically initiate from the pericycle
   - a. at sites of starch accumulation.
   - b. at the protoxylem poles.
   - c. between metaxylem cells.
   - d. directly from the phloem.
   - e. near endodermal passage cells.

7. The development of lateral roots is said to be
   - a. endogenous.
   - b. exogenous.

8. Cells of the columella
   - a. are derived from procambium.
   - b. are meristematic.
   - c. are adapted for absorption.
   - d. possess statoliths.
   - e. are derived from ground meristem.

9. The root vascular cambium arises from the
   - a. endodermis.
   - b. exodermis.
   - c. phellogen.
   - d. pith.
   - e. pericycle.

10. In biological nitrogen fixation and mycorrhizal associations, the microbe receives __________ and the plant receives __________.
    - a. minerals … water.
    - b. ions … carbohydrates.
    - c. photosynthate … nitrogen or phosphate.
    - d. nitrogen … phosphate.
    - e. carbohydrate … ions.

? 11. A velamen is
   a. formed inside of an exodermis.
   b. a multiple rhizodermis.
   c. characterized by containing a Casparian strip.
   d. found in underground storage roots.
   e. composed of densely cytoplasmic cells upon maturity.

Concept Applications

? 12. It is very common in the horticultural trade to propagate plants via stem cuttings. Explain how a piece of stem can be used to regenerate an entire plant—stems, roots, and leaves. Why couldn't root cuttings be used in a similar fashion?

? 13. Growing tomato plants upside down in hanging buckets is quite the rage. Research and write a minute paper on the role root gravitropism plays in plants growing upside down.

References and Additional Readings

Blancaflor EB, Fasano JM, Gilroy S (1998) Mapping the functional roles of cap cells in the response of *Arabidopsis* primary roots to gravity. Plant Physiol 116:213–222

Chomicki G, Bidel LPR, Ming F, Coiro M, Zhang X, Wang Y, Baissac Y, Jay-Allemand C, Renner SS (2014) The velamen protects photosynthetic orchid roots against UV-B damage, and a large dated phylogeny implies multiple gains and losses of this function during the Cenozoic. New Phytol 205:1330–1341

Crang RFE, Vassilyev A (2003) Electronic Plant Anatomy. McGraw-Hill, New York

Cutler DF, Botha T, Stevenson D (2008) Plant Anatomy: An applied approach. Blackwell Publishing, Malden

Dickinson WC (2000) Integrative Plant Anatomy. Hardcourt, Inc., Orlando

Dietrich D, Pang L, Kobayashi A et al (2017) Root hydrotropism is controlled via a cortex-specific growth mechanism. Nature plants 3:17057. https://doi.org/10.1038/nplants.2017.57

Ercolin F, Reinhardt D (2011) Successful joint ventures of plants: arbuscular mycorrhiza and beyond. Trends Plant Sci 16:356–362

Esau K (1953) Plant Anatomy. Wiley, New York

Esau K (1977) Anatomy of Seed Plants. Wiley, New York

Evert RF (2006) Esau's Plant Anatomy: Meristems, cells and tissues of the plant body — Their structure, function and development, 3rd edn. Wiley, Hoboken

Fahn A (1990) Plant Anatomy, 4th edn. Pergamon Press, New York

Fox JE, Gulledge J, Engelhaupt E, Burow ME, McLachlan JA (2007) Pesticides reduce symbiotic efficiency of nitrogen-fixing rhizobia and host plants. Natl Acad Sci, Proc 104:10282–10287

Garrett TY, Huynh C-V, North GB (2010) Root contraction helps protect the "living rock" cactus *Ariocarpus fissuratus* from lethal temperature when growing in rocky soil. Amer J Bot 97:1951–1960

Gray A (1887) The Elements of Botany for Beginners and Schools. American Book Co., New York, 226 pp

Grierson C, Nielsen E, Ketelaar T, Schiefelbein J (2014) Root hairs. The Arabidopsis Book. Amer Soc Plant Biol. https://doi.org/10.1199/tab.0172

Hearn DJ, Poulsen T, Spicer R (2013) The evolution of growth forms with expanded root and shoot parenchymatous storage is correlated across the eudicots. Intl J Plant Sci 174:1049–1106

Jackson MB (2002) Long-distance signaling from roots to shoots assessed: the flooding story. J Exptl Bot 53:175–181

Kaplan I, Halitschke R, Kessler A, Rehill BJ, Sardanelli S (2008) Physiological integration of roots and shoots in plant defense strategies links above- and belowground herbivory. Ecol Lett 11:841–851

Martin F, Kohler A, Murat C, Veneault-Fourrey C, Hibbett DS (2016) Unearthing the roots of ectomycorrhizal symbioses. Nature Rev Microbiol 14:760–773

Mauseth JD (1988) Plant Anatomy. Benjamin/Cummings, Menlo Park

Metcalfe CR, Chalk L (1979) Anatomy of the Dicotyledons: Vol 1, Systematic anatomy of the leaf and stem, 2nd edn. Oxford Univ Press, New York

Metcalfe CR, Chalk L (1983) Anatomy of the Dicotyledons: Vol 2, Wood structure and conclusion of the general introduction, 2nd edn. Oxford University Press, New York

Purnobasuki H, Suzuki M (2005) Aerenchyma tissue development and gas-pathway structure in root of *Avicennia marina* (Forsk.) Wierh. J Plant Res 118:285–294

Ryan E, Steer M, Dolan L (2001) Cell biology and genetics of root hair formation in *Arabidopsis thaliana*. Protoplasma 215:140–149

Solereder H (1908a) Systematic Anatomy of the Dicotyledons: A handbook for laboratories of pure and applied botany, vol 1. Clarendon Press, Oxford

Solereder H (1908b) Systematic Anatomy of the Dicotyledons: A handbook for laboratories of pure and applied botany. Vol. 2, Monochlamydea, addenda, and concluding remarks. Clarendon Press, Oxford

Steffens B, Rasmussen A (2016) The physiology of adventitious roots. Plant Physiol 170:603–617

Takei K, Takahashi T, Sugiyama T, Yamaya T, Sakakibara H (2002) Multiple routes communicating nitrogen availability from roots to shoots: a signal transduction pathway mediated by cytokinin. J Exptl Bot 53:971–977

Torres-Cortés G, Ghignone S, Bonfante P, Schüßler A (2015) Mosaic genome of endobacteria in arbuscular mycorrhizal fungi: Transkingdom gene transfer in an ancient mycoplasma-fungus association. Proc Natl Acad Sci 112:7785–7790. https://doi.org/10.1073/pnas.1501540112

Tromp J (1983) Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen. Plant Soil 71:401–413

Vriet C, Smith AM, Wang TL (2014) Root starch reserves are necessary for vigorous re-growth following cutting back in *Lotus japonicus*. PLoS One 9(1):e87333. https://doi.org/10.1371/journal.pone.0087333

Wullschleger SD, Meinzer FC, Vertessy RA (1998) A review of whole-plant water use studies in trees. Tree Physiol 18:499–512

York LM, Carminati A, Mooney SJ, Ritz K, Bennett MY (2016) The holistic rhizosphere: integrating zones, processes, and semantics in the soil influenced by roots. J Exptl Bot 67:3629–3643

Zotz G, Winkler U (2013) Aerial roots of epiphytic orchids: the velamen radicum and its role in water and nutrient uptake. Oecologia 171:733–741