C1 Meristems and primary tissues

Key Notes

Meristems

Meristems form the new cells of a plant. Apical meristems occur near the tips of roots and shoots and give primary growth. They give rise to the epidermal tissue, vascular tissue and ground meristems that form the parenchyma. Intercalary meristems are formed at the nodes of grass stems. Lateral meristems generate secondary growth. The vascular cambium is a cylinder that forms new phloem and xylem. The cork cambium is also a cylinder, that forms the bark.

Tissues and organs

A tissue is a collection of cells with common function. It may be simple or complex. An organ is a multicellular functional unit. Plant organs are made of three types of tissue: dermal, vascular and ground.

Ground tissues

Ground tissue is made up of parenchyma, collenchyma and sclerenchyma. Mature parenchyma cells have large vacuoles and intercellular spaces. Leaf parenchyma cells with chloroplasts are chlorenchyma. Collenchyma cells have strong cell walls providing support. Sclerenchyma also provides support. It is made up of dead cells with a thickened, lignified secondary wall, in sclereids (small groups of cells) or fibers (long strands of elongate cells).

Dermal tissue

The outer most cell layer is known as the epidermis. It is formed of parenchyma-like cells and specialized cells for transport of gases, water and nutrients.

Vascular tissue

Vascular tissue is made up of xylem and phloem. Xylem carries water and dissolved minerals, and phloem the solutes from sites of synthesis to sites of storage or use. Xylem cells have thickened secondary cell walls and no cell contents. Xylem vessel elements join to form vessels. Tracheids are tapered cells that interconnect via pits. Phloem has two cell types: sieve tube elements and companion cells. Sieve tube elements have no nucleus, but contain organelles and link through sieve plates. Companion cells are narrower than sieve tubes and function with them.

Related topics

The cell wall (B2)
Features of growth and development (F1)
Plants and water (I1)

Meristems

Meristems are the site of formation of new cells within the plant (*Fig. 1*). **Apical meristems** occur near the tips of roots and shoots and give length increase (**primary growth**). They contain **initials**, the equivalent of stem cells in animals, which retain the ability to divide and generate new cells throughout the life of the meristem. They form **primary meristems** that produce the tissues of the stem and root. These primary meristems are the **protoderm** (which forms the **epidermis** or outer cell layer of the shoot), the **procambium** (which forms **phloem** and **xylem**, see 'Vascular tissue' below), and the **ground meristems** (which form **parenchyma**). Grasses have **intercalary meristems** close to the nodes of the stem (the point where leaves attach) which are also responsible for length increase.

Lateral meristems give increase in girth (**secondary growth**). The **vascular cambium** (sometimes known just as **cambium**) is a cylinder of cells that forms new phloem and xylem (see 'Vascular tissue' below). New cells formed by the cambium are termed **derivatives**, while those that remain to divide again are **initials**. The **cork cambium** is a meristematic tissue found in woody plants. It is a cylinder of cells, located beneath the bark, which it forms (*Fig. 1*).

Tissues and organs

A **tissue** is a collection of cells with common function. It may be **simple**, made of one cell type or **complex**, made of several cell types. An organ is a collection of tissues with a specific function such as flowers, roots and leaves. Plant organs are made of three types of tissue: **dermal** (the epidermis or outer cell layer),

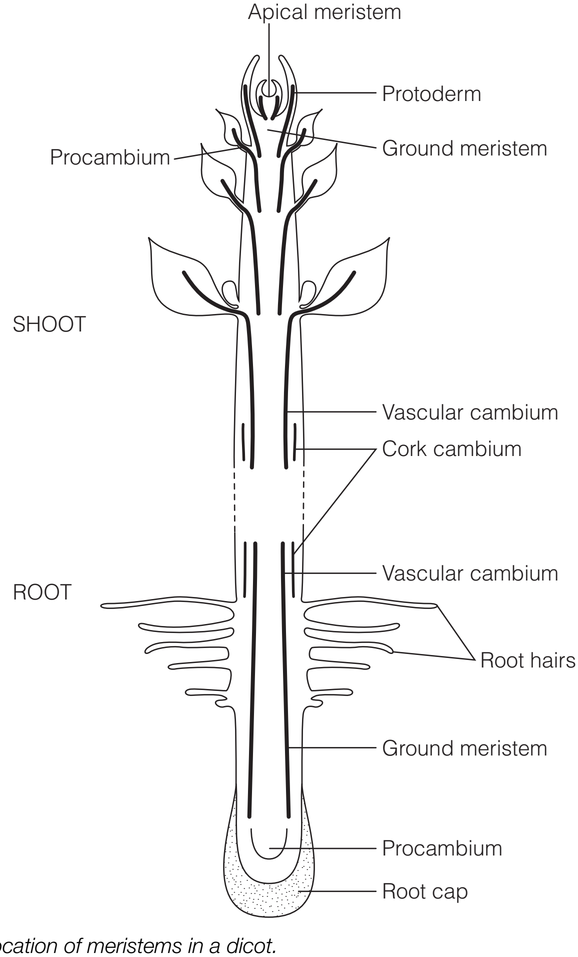


Fig. 1. The location of meristems in a dicot.

vascular (transport tissue) and **ground** (all the remaining cells). The type and quantity of each tissue varies for each organ.

Ground tissues

Ground tissues lie under the epidermis and contribute to structural strength and function. **Parenchyma** cells are the most abundant cell types found throughout the plant and form the bulk of organs such as leaves, roots and stems. They are formed with thin flexible cell walls and are initially cuboid, later becoming nearly spherical or cylindrical. As they form mature tissue, their shape is constrained by surrounding cells. In a typical parenchyma tissue, cells are joined at the points of contact, but there are frequent large **intercellular spaces**. This means they take a variety of shapes. Parenchyma cells have large vacuoles, and parenchyma are frequently storage tissues for starch and other food reserves and for water. Leaf parenchyma cells are photosynthetic, have chloroplasts and are called **chlorenchyma**. **Aerenchyma** is a parenchyma tissue found in some species in which some cells are lost to form large gas-spaces. These promote buoyancy in some aquatic species or supply oxygen to the growing tip of roots in waterlogged soil. Parenchyma cells often retain the ability to divide when the plant is wounded, forming a **callus** (an amorphous mass of cells; see Topic F1) which fills the wound site and may eventually form new tissues to repair the wound.

Collenchyma is made up of living cells which are similar to parenchyma, but with stronger, unevenly thickened cell walls. Collenchyma cells are often found as flexible support beneath the epidermis of growing tissues and in many other locations, including stems, leaves and fruits. Cotton is a fabric made of plant collenchyma tissue.

Sclerenchyma is a supporting tissue found in organs which have completed lateral growth. It is made up of dead cells with even, lignified secondary cell walls either in **sclereids** (small groups of cells) or **fibers** (long strands of elongate cells). Plant fibers have been widely used in textiles and rope making.

Dermal tissue

All organs are surrounded by a layer of cells, the **dermal tissue** that forms a protective covering, known as the **epidermis**. It consists of parenchyma or parenchyma-like cells and usually forms a complete covering, except where specialized pores (e.g. for gas exchange; see Topic I2) are present. The epidermis protects the tissues beneath from mechanical damage and pathogens (Topic M4). The root epidermis (or **rhizodermis**) is specialized for the absorption of mineral nutrients and water (Topics I1 and I4).

Vascular tissue

Xylem and **phloem** together make up the **vascular tissue**, the conducting tissues for fluids through the plant (*Fig. 2*). Xylem carries predominantly water and dissolved minerals from root to shoot (Topics I1 and I4); phloem carries solutes like sugars and amino acids from sites of synthesis or storage (sources) to sites of storage or use (Topic J4).

Xylem cells have lost their cellular contents, and have unevenly thickened secondary cell walls that are strengthened with lignin. There are two main types of xylem cells. **Vessel elements** are elongate, open-ended cells which lose their end walls to form continuous pipes (**vessels**). **Tracheids** are tapered cells, with overlapping ends and often spiral thickening of the cell wall. Rather than being open-ended, perforations or pits allow water to move from one cell to another. The first formed xylem cells are known as **protoxylem**. They have helical or annular secondary thickening, so the cells can elongate when stretched by the

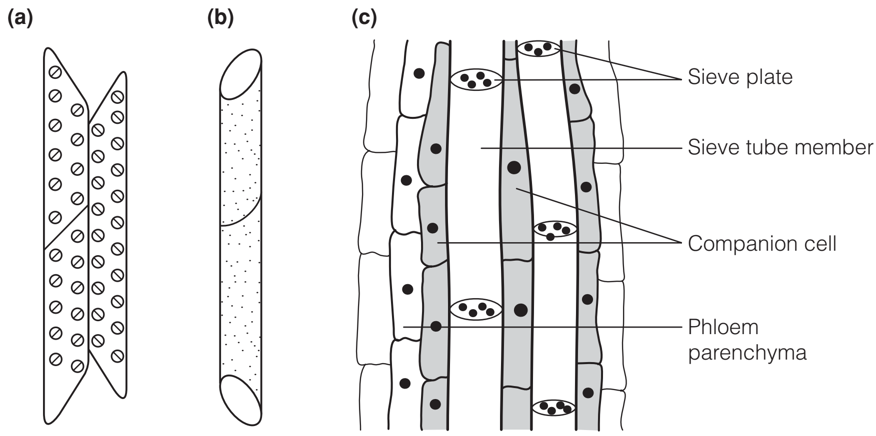


Fig. 2. Structure of phloem and xylem.

surrounding tissue. Metaxylem cells form after elongation has ceased and have more complex secondary thickening. **Ray cells** radiate from the vascular cambium of roots or stems of woody plants and permit lateral movement of water.

Phloem tissue has two cell types. **Sieve tube** members form an elongated pipe, the sieve tube. The cells are living and are linked through perforations in adjoining end cell walls (the **sieve plate**). The cytoplasm of these adjoining cells also connects, and transport of solutes takes place through it (Topic H4). Sieve tube members have no nuclei, but retain other functional organelles. The other cell type is the **companion cell**, which have many mitochondria and provide energy required for phloem transport (Topic J4).

C2 ROOTS

Key Notes

Primary structure

The tip of a root is protected by a root cap behind which is a meristem and elongation zone. Nutrient and water uptake occurs through root hairs, formed as protrusions of epidermal cells in the maturation zone. The vascular cylinder becomes mature in this zone, with a water-impermeable endodermis and functional phloem and xylem.

Root apical meristems

Closed roots have three layers of cells (initials) in the apical meristem which form all the tissues present. Open roots have three meristems close to the apical meristem: the procambium which forms the vascular cylinder, the ground meristem which forms the cortex and the protoderm which forms the epidermis.

Root cap

The root cap is a cone of cells which protects the meristem and secretes mucilage. Root cap cells are constantly sloughed off. The mucilage provides an environment for bacteria and fungi which live in the rhizosphere, the immediate environment of the root.

Root hairs

Root hairs are outgrowths of epidermal cells giving a high surface area of contact with the soil for water and mineral nutrient uptake. They are short-lived and the mature regions of the root are hair-less.

Root architecture

The primary root persists as a taproot and lateral roots arise from it in many plants, though in monocots it dies and adventitious roots grow from the stem. These give rise to a mass of fine, fibrous roots, all of similar size. Root architecture is responsive to soil depth, water availability and nutrients.

Related topics

Meristems and primary tissues (C1)
Plants and water (I1)
Uptake of mineral nutrients in the plant (I4)

Primary structure

Roots extract water and minerals from soil. They penetrate the soil, growing by elongation near the tip. As soil is a resistant medium, the growing tip has a near conical protective **root cap** (*Fig. 1*) which lubricates the root surface as it is pushed by cell expansion between soil particles. Growth occurs when new cells, formed in meristems in the **zone of cell division** elongate in the **elongation zone** (*Fig. 1*). This elongation is driven by **hydrostatic pressure** within the cell (Topic I1) that propels the root tip deeper into the soil. The elongation zone is effectively cylindrical, allowing growth in the soil. Behind it, in the **maturation zone**, root hairs develop which provide large areas of contact with the water and nutrient films surrounding soil particles and anchor the older parts of the root.

Internally, the ground tissue of the root is the **cortex**, made up of large, vacuolate cells which fill the space between the epidermis and **vascular cylinder** (**stele**). While all the cells in the root can be traced back to their origins in the root meris-

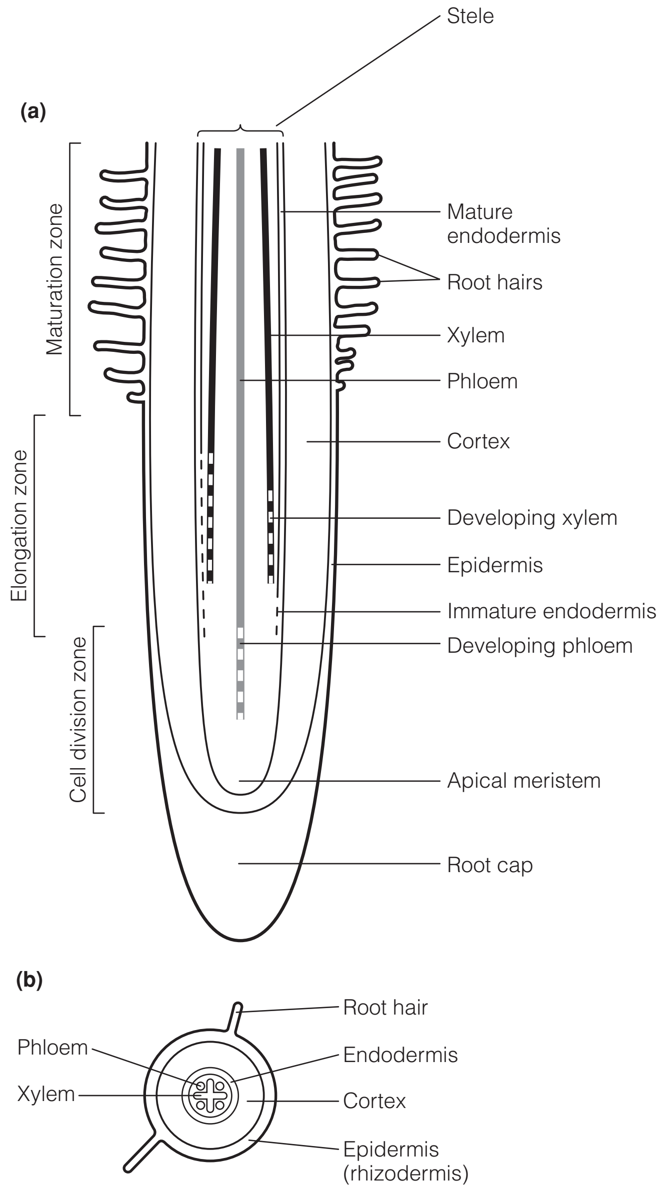


Fig. 1. (a) A generalized representation of a longitudinal section of a typical root. (b) The transverse section is from the maturation zone and is of a root with four groups of xylem cells forming a cross-like appearance. This is known as a tetrarch root; other species are diarch (two), triarch (three) or more.

tems (see below), many of the key tissues of the root cannot be observed until they form in the maturation zone (*Fig. 1*). The vascular bundle (stele) contains phloem (which develops first) and xylem surrounded by a cylinder of cells with water-resistant cell walls, the **endodermis** (Topic I4). Endodermal cells possess a characteristic thickening of the **anticlinal cell walls** (radial and transverse walls, which are perpendicular to the root surface). This wall thickening, the **Casparian strip**, is impregnated with a water-impermeable substance, **suberin**.

Immature xylem and endodermis can be observed below the area where root hairs form (*Fig. 1*). Later, above the root hair zone, **lateral roots** may form. These originate in the cells near the vascular tissue and force their way out through the cortex and epidermis. Each lateral root has a meristem and its vascular tissue interconnects with that of the primary root.

Root apical meristems

The meristem lies behind the root cap and comprises small, thin-walled cells with prominent nuclei and no large vacuole (Topic C1). Two types of root have been suggested. In **closed roots** (for instance in corn [maize]; *Fig. 2a*), three layers of cells (**initials**) can be identified in a single region in the **apical meristem**, which form all the tissues of the root. In the second type, **open roots** (for instance onion; *Fig. 2b*), there appear to be three meristems which separately form the tissues of the root.

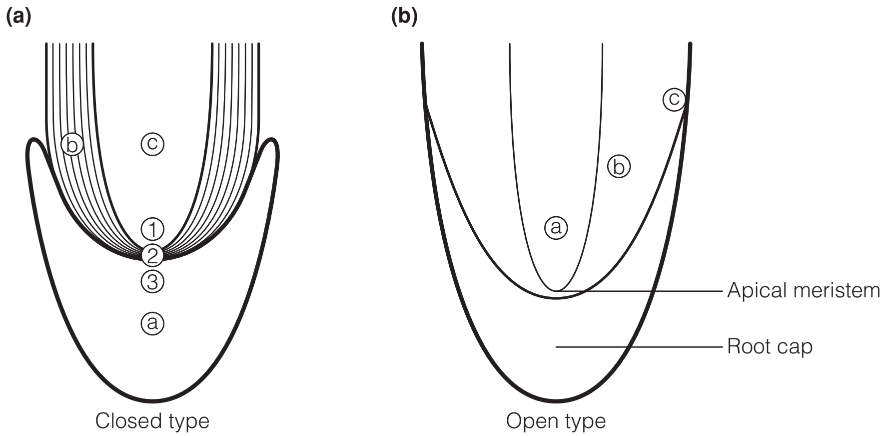


Fig. 2. (a) Closed and (b) open roots. Closed roots have a single region of cell division where three layers of cells (initials; 1, 2, 3) give rise to the epidermis (a), the cortex (b) and the vascular cylinder (c). In an open root, there are three separate meristems near the apical meristem. The procambium (a) gives rise to the vascular cylinder; the ground meristem (b) gives rise to the cortex; and the protoderm (c) gives rise to the epidermis.

Root cap

The **root cap** is a conical collection of parenchyma cells, which in some plants is large and conspicuous and in others small. It protects the root tip as it is forced through the soil and secretes **mucilage** as lubricant made in the Golgi apparatus of **slime-secreting cells**. Root cap cells have a short life (up to 1 week, depending on species) and are constantly sloughed off and may remain alive in the mucilage for some time. The mucilage provides an environment for bacteria and fungi which live in the **rhizosphere**, the immediate environment of the root.

Root hairs

Root hairs are single cell structures formed as outgrowths of epidermal cells (*Fig. 3*). They form a **root hair zone** that gives a very high surface area of contact with the soil. While root hairs are normally only 0.1–1.0 cm long, they can be extremely numerous, with more than 20 000 hairs cm^{-2} of root and billions per plant, giving a vast surface area for absorption. Root hairs are also short-lived and the mature regions of the root are hair-less. The root hair zone is therefore extremely important for water and mineral nutrient uptake, though in plants with mycorrhizal fungi (Topic M1) associated with the root, root hairs may be much less important or absent.

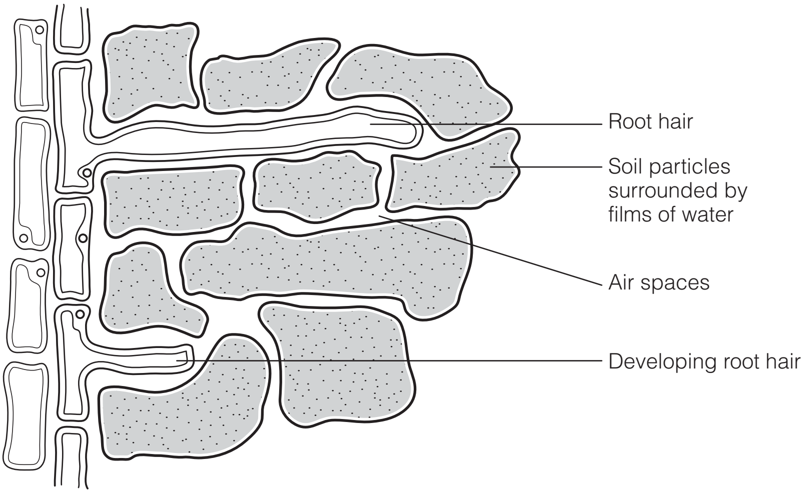
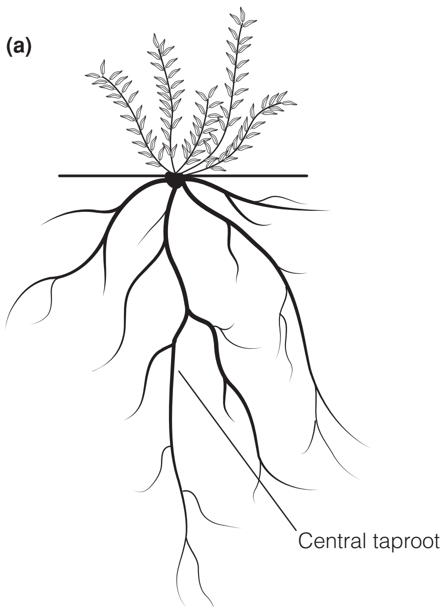


Fig. 3. Root hairs. A root hair forms as an outgrowth of an epidermal cell and is a unicellular structure.

Root architecture

All plants first form a **primary root** and in most plants, including the gymnosperms, primitive dicotyledons and eudicotyledons this persists as a **taproot**. The **lateral roots** arise from it at various points (*Fig. 4a*). In the monocotyledons the primary root dies and **adventitious roots** are formed which grow out of the stem. These give rise to a mass of fine, **fibrous roots**, all of similar size and prominence (*Fig. 4b*). Root architecture always follows one of these basic plans, but is also responsive to soil depth, water availability and nutrients.

(a)



(b)

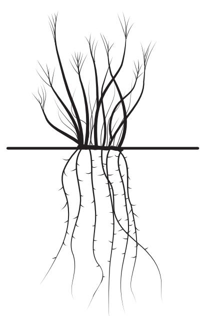


Fig. 4. Root architecture. (a) Taproot systems result when lateral roots branch out from a single central taproot. (b) Fibrous roots form from adventitious roots, branching out from the stem base.

C3 Herbaceous stems and primary growth

Key Notes

Shoot structure

Herbaceous stems are green and non-woody. They have a range of growth forms generated by an apical meristem that produces leaf and bud primordia. The shoot is surrounded by an epidermis, within which lies the cortex. Vascular tissues occur as a ring of separate bundles towards the outside of the stem in dicotyledons and in a scattered pattern in monocotyledons. The center of the stem is the pith parenchyma.

Meristems

The shoot meristem has a tunica producing the epidermis and the layers of cells beneath it while the corpus produces the cortex, pith and vascular tissues. The meristem can also be divided into the central zone where cell division occurs, the peripheral zone where leaves, shoots and new meristems form, and the rib zone where stem growth occurs.

Vascular tissue

Vascular bundles containing phloem and xylem form a ring or a complex array throughout the inner part of the stem. In some dicotyledons the ring is almost continuous.

Architecture

The shape of the stems is governed by the controlled positioning of leaves and buds by the meristem. Their positioning may be spiral, distichous, opposite, decussate or whorled.

Related topics

Meristems and primary tissues (C1)
Woody stems and secondary growth (C4)
Features of growth and development (F1)

Shoot structure

Herbaceous stems are green throughout without deposition of lignin that would make them woody. Shoots are more complex than roots and take on a wide range of growth forms reflecting function. Like the root, the shoot has an **apical meristem**. Unlike the root (where lateral branching only occurs in mature tissue), the shoot meristem produces lateral shoots and leaves (*Fig. 1*).

The apical meristem produces **leaf primordia** (which will form leaves) and **bud primordia** (which will form shoots). These are produced in position and order which gives rise to the characteristic form of the shoot which is recognizable for each species (see 'architecture' below).

The shoot is surrounded by an **epidermis.** This outer layer provides the protective barrier between the stem and its environment and is covered in a lipid-based protective substance, cutin (Topics I1 and M4). Within the epidermis, cells of the **ground tissues**, the **cortex**, may be photosynthetic and occupy the space surrounding the **vascular bundles**. In some species, the cortex is only a few cell layers, in others many more. Within the cortex, bounded by the vascular bundles, the center of the stem is occupied by **pith** (*Fig. 2*).

Meristems

The shoot meristem produces the cells that will form the major tissues of new stems and leaves. It is organized in layers of cells each producing a different tissue and in zones with different functions (*Fig. 3*). **Layer 1** produces the epidermis that surrounds the shoot. Here cells divide to generate only a single layer. Beneath it, **layer 2** divides to generate the layers of cells beneath the epidermis. Layer 1 and layer 2 together are known as the **tunica**. **Layer 3** produces all the other tissues of the shoot: the cortex, pith and vascular tissues,

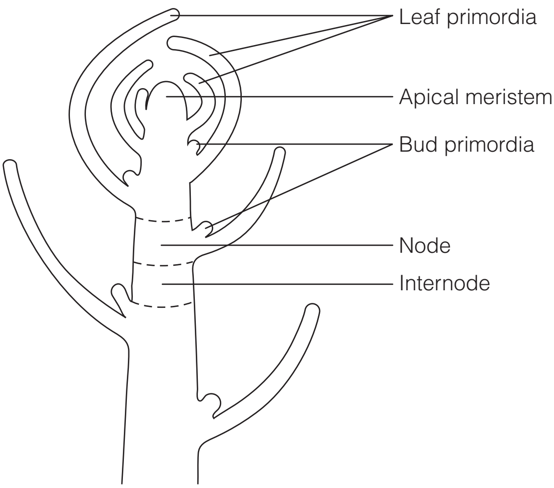


Fig. 1. A longitudinal section of a simplified dicot stem.

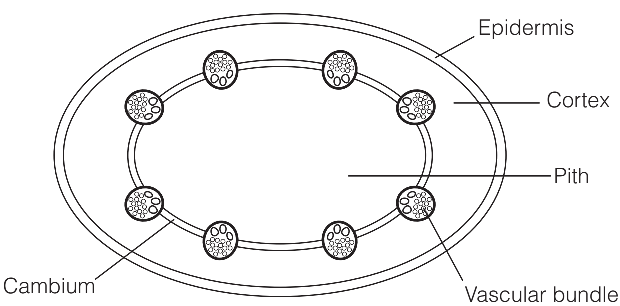


Fig. 2. A transverse section of a simplified dicot stem, showing the vascular bundles containing phloem and xylem arranged in a cylinder and separated by interfascicular cambium.

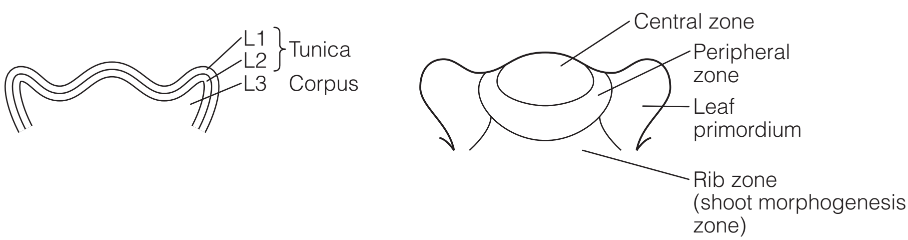


Fig. 3. A schematic representation of a longitudinal section through a shoot apical meristem. Layer L1 forms the epidermis, L2 the cell layers beneath the epidermis and L3 the pith, cortex and vascular tissue. (Redrawn from R. Twyman (2001), Instant Notes in Developmental Biology, *BIOS Scientific Publishers Ltd.)*

and is known as the **corpus**. The **central zone** contains actively dividing cells. Leaves and shoots (including new meristems) form in the **peripheral zone**. Stem growth occurs in the **rib zone** and cells mature to form the tissues of the shoot.

Vascular tissue

The vascular tissue of the shoot commonly occurs as a ring of separate vascular bundles, each containing **phloem** and **xylem**. They are located between the cortex and pith (*Fig. 2*) in dicotyledons, while in monocotyledons they are found in a scattered array throughout the inner part of the stem. All vascular bundles contain phloem and xylem strands in parallel to one another. Associated with the xylem strands are **xylem parenchyma** cells and fibrous **sclerenchyma** tissue may be associated with the phloem. In some dicotyledons, the vascular bundles form an almost continuous ring; however, individual vascular bundles remain, separated by narrow bands of **interfascicular parenchyma** (the site of origin of the cambium for secondary growth) which separate the cortex from the pith (*Fig. 2*).

Architecture

The shape of the stems of different species are clearly recognizable from one another (*Fig. 4*). For instance, before flowering, *Arabidopsis thaliana* (Topic E1) forms a **rosette** of leaves, each initiated 137.5° from the preceding one formed. This process, termed **spiral** (or helical) **phyllotaxy**, is common in many species and results in the formation of a spiral pattern of growth. In other species, new leaves may be formed singly at each node in two opposite rows (**distichous phyllotaxy**), in pairs opposite one another (**opposite phyllotaxy**) or in whorls of five or more at one node (**whorled phyllotaxy**). Where pairs of leaves form at right angles to a previous pair of leaves, the plant has **decussate phyllotaxy**.

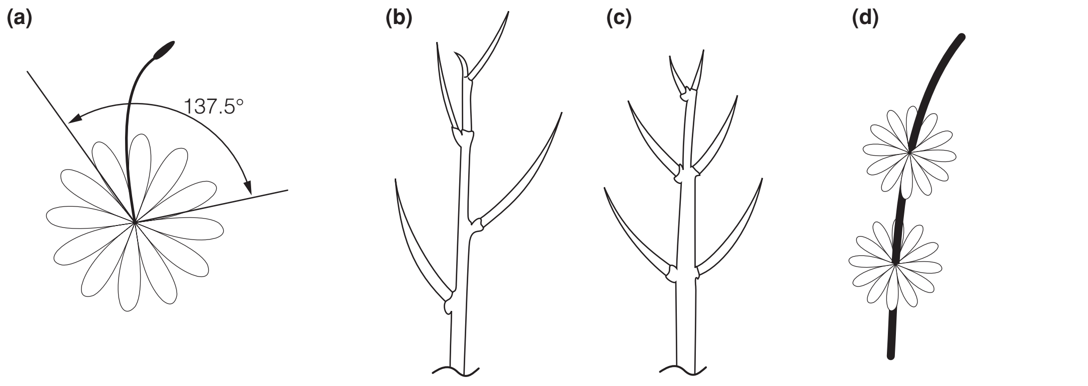


Fig. 4. Forms of phyllotaxy. (a) spiral phyllotaxy, (b) distichous phyllotaxy, (c) opposite phyllotaxy, (d) whorled phyllotaxy.

C4 WOODY STEMS AND SECONDARY GROWTH

Key Notes

Secondary growth

Secondary tissues are formed by secondary meristems and give increases in diameter and strength. Secondary tissues are frequently woody, strengthened by deposition of lignin, a polymeric phenolic compound, mostly in secondary cell walls.

Vascular cambium and cork cambium

Increase in diameter results from the action of the vascular cambium and the cork cambium. The vascular cambium lies between the primary phloem and xylem and divides to form phloem on the outside and xylem on the inside. The cork cambium lies within the stem cortex and generates cells filled with suberin. Gas exchange occurs through lenticels where stomata once were.

Wood anatomy

The center of a tree trunk contains heartwood, where the vascular system no longer functions. Around it lies the sapwood that contains functional phloem and xylem. Vascular rays of long-lived parenchyma cells radiate across the trunk, conducting nutrients and water. Bark is made up of the outermost layers of the trunk, including cork and outer phloem cells.

Related topics

Meristems and primary tissues (C1)
Herbaceous stems and primary growth (C2)
Features of growth and development (F1)

Secondary growth

Many species of plant complete their life cycle using only the primary tissues generated by primary meristems. These are the herbaceous species described in Topic C3. In many other species, production of primary tissue and elongation growth are followed by the deposition of **secondary tissue**. These tissues give increases in diameter and the tissues formed are strengthened in comparison to primary tissues by deposition of extensive secondary walls and **lignin**, a polymeric phenolic compound, in the cell wall making them **woody**. Plants showing secondary growth usually live for many years, the wood making them resistant to damage by herbivores and weather. Monocots do not normally generate secondary tissues, but some, like palm trees, undergo additional primary growth to form thick stems. Some palms also continue cell division in older parenchyma tissue to give what is known as diffuse secondary growth.

Vascular cambium and cork cambium

Increase in diameter results from the action of two secondary meristems, the **vascular cambium** and the **cork cambium**. The vascular cambium is a narrow band of cells between the primary phloem and xylem (*Fig. 1*), which remains a meristem. This tissue goes on dividing indefinitely with active growth in spring and early summer in temperate trees, with the new cells being formed to the

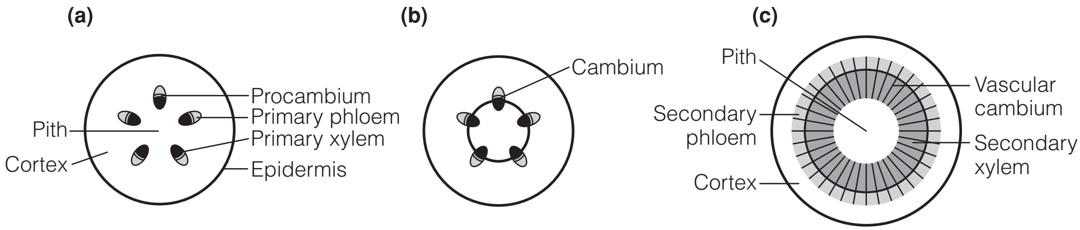


Fig. 1. Development of a woody angiosperm stem. When primary growth is complete, the stem has a number of vascular bundles with procambium separating primary phloem and xylem (a). At the onset of secondary growth, this cambium forms a ring (b) which develops into the vascular cambium which generates secondary xylem on its inner, and secondary phloem on its outer face (c).

outside of the cambium to form phloem and the inside to form xylem (*Fig. 2*). The newly formed **secondary phloem** and **xylem** function like the primary vascular tissue in transport. As xylem cells are deposited on the inner face, the vascular cambium moves outwards. In temperate regions early in the growing season, the cambium produces xylem cells of large diameter and these get progressively smaller as the season progresses. In consequence, growth appears as more and less dense bands of cells, the familiar **annual rings** observed in cross section of a tree trunk. Some tropical species on the other hand, such as ebony, produce xylem consistently throughout the growing season and their wood is of a consistent appearance without annual rings, though many species of the seasonal tropics have annual cycles similar to those of temperate trees.

The cork cambium arises within the stem cortex and generates cuboid cells that quickly become filled with the waxy substance **suberin** (also found as water-proofing in the root endodermis; Topic I1). Suberinized cells die, but the dead cells remain as a protective layer (*Fig. 3*), required because the original epidermis can no longer function. **Cork tissue** forms part of the **bark** of the tree (the remainder being secondary phloem) and replaces the epidermis. Its character and thickness varies from species to species. Some gas exchange to the stem occurs through **lenticels**, pores remaining through the bark.

Wood anatomy

If a transverse section of a tree trunk is studied (*Fig. 3*), a number of features appear. Concentric circles of annual growth rings are evident in most trees from

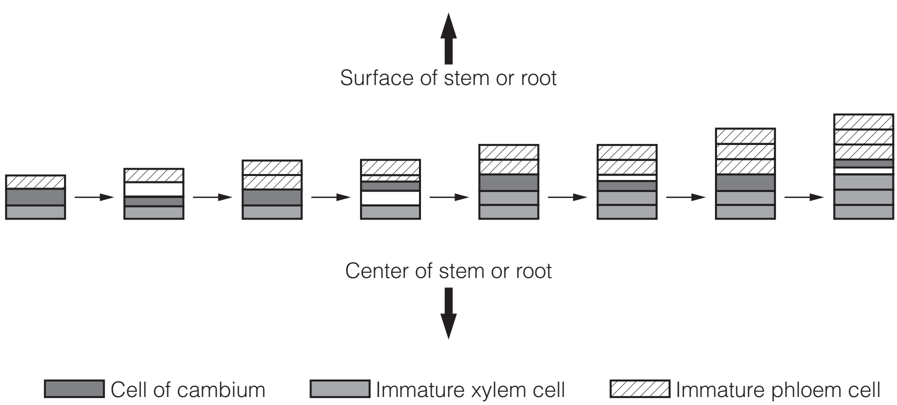


Fig. 2. The cells of the vascular cambium divide to form secondary phloem to the outside and secondary xylem to the inside. (Redrawn from Stern, K.R. (2000) Introductory Plant Biology, *8th Edn, McGraw-Hill Publishing Company.)*

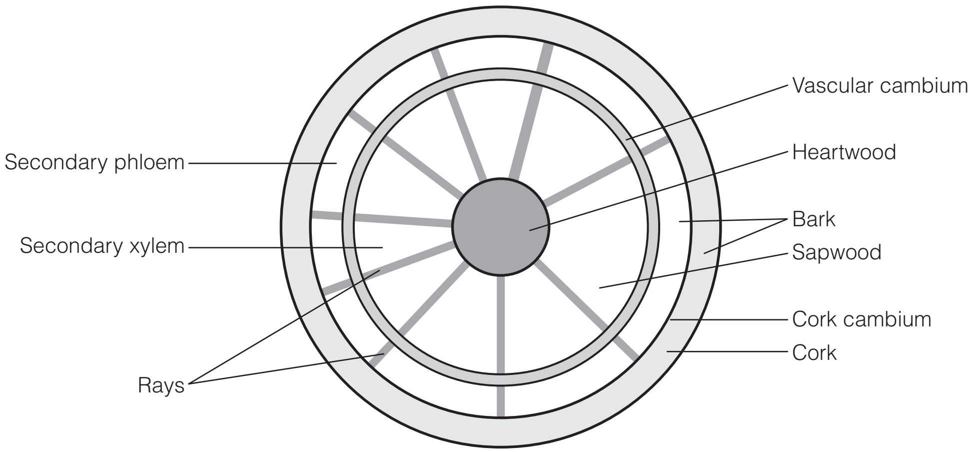


Fig. 3. A transverse section of a woody stem, showing the major layers of heartwood, sapwood and bark.

seasonally varying environments. The center of the trunk of many species is the **heartwood**, where the vascular system no longer functions. It provides structural support and is often darker and impregnated with tannins (Topic J5), but may be completely removed without killing the tree. Around the heartwood lies the **sapwood** that contains functional phloem and xylem. **Vascular rays** radiate from the center of the trunk. These are formed of long lived parenchyma cells which conduct nutrients and water across the trunk, crossing both phloem and xylem, and are responsible for secretions into the heartwood.

The outermost layers of the trunk are known as **bark**. Bark includes the **corky tissues** produced by the cork cambium and the underlying layers outside the vascular cambium, including the secondary phloem.

C5 Leaves

Key Notes

Leaf types

Leaves are the main photosynthetic organs of plants. The leaf blade lamina generally has a large surface area to maximize light capture and may have a petiole. Compound leaves have a lamina divided into leaflets and a central rachis. The lamina may be much reduced (e.g. in conifer needles). The vascular tissue of the leaf occurs as veins, which are branched from a central midrib forming a network, or are parallel to one another.

General leaf structure

A typical dicot leaf has upper and lower surfaces protected by the epidermis with a waxy cuticle and may have leaf hairs. The photosynthetic cells are the palisade and spongy mesophyll. Both cell types are surrounded by gas spaces. Carbon dioxide enters these by way of stomatal pores in the epidermis connecting with the gas spaces of the mesophyll. Transport to and from the leaf occurs in veins which contain xylem and phloem.

Other types of leaf

Some species show Krantz anatomy in which the mesophyll surrounds bundle sheath cells around the vascular bundle in a ring. Leaves adapted to drought may be thickened and fleshy with a low surface area. Conifer needles have a small surface area, sunken stomata, a hypodermis beneath the epidermis and an endodermis surrounding the vascular tissue.

Related topics

Plastids and mitochondria (B3)
Herbaceous stems and primary growth (C3)
Features of growth and development (F1)
Water retention and stomata (I2)
C3 and C4 plants and CAM (J3)

Leaf types

The major photosynthetic organ of most plants is the **foliage leaf** (*Fig. 1*). This is mainly made up of cells containing chloroplasts. They are generally flat and thin with a lamina of large surface area attached to the plant by a stalk or **petiole**. The structure is arranged so that both the leaf lamina and the chloropasts can be orientated to the sunlight. The lamina is commonly thin so that light does not have to penetrate far (losing energy) before it impinges on a chloroplast. However, such large, flat surfaces are easily desiccated or damaged and a variety of leaf adaptations exists.

Leaves with a stalk or **petiole** are **petiolate**. A lamina without a petiole is a **sessile** leaf. Some monocotyledons, such as the grasses, have a long narrow leaf blade without a petiole, the base of which forms a sheath around the stem. In some species, the lamina is divided into smaller leaflets, forming a **compound leaf**. In these, the petiole is extended to form a **rachis**, with **leaflets** (*Fig. 2*). The vascular tissue of the leaf appears as **veins,** which give strength and rigidity**.** Most dicots and some monocots have a prominent central midrib and a network of veins

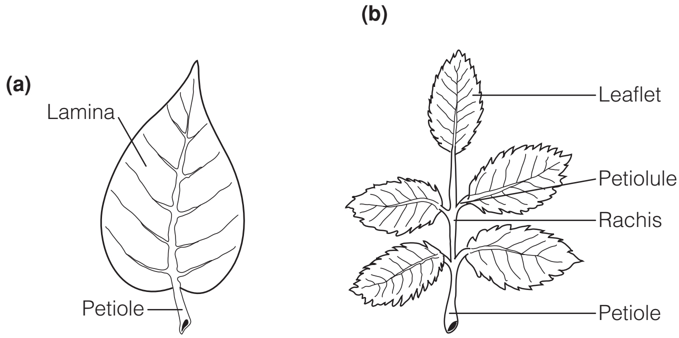


Fig. 1. (a) A simple and (b) compound leaf showing the names of the major structures of the leaf.

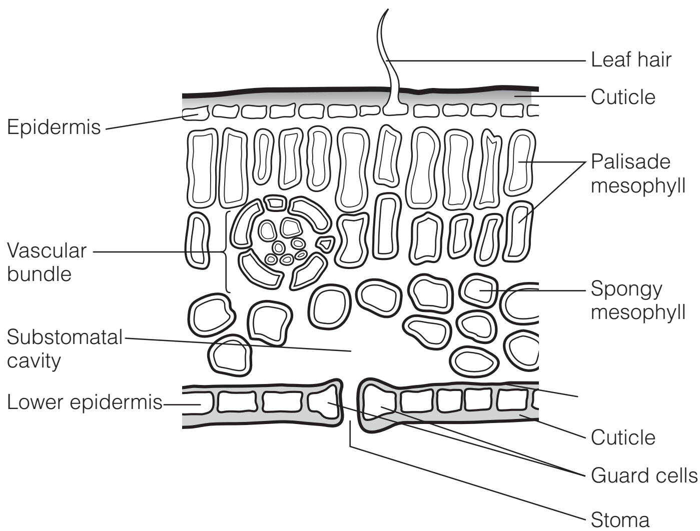


Fig. 2. A transverse section of a leaf, showing the major tissues and cell types present. Note the photosynthetic tissues of the palisade and spongy mesophyll.

around this; others have several parallel veins. In conifers, the leaf is reduced to a **needle** or scale with a single vascular strand and much reduced surface area.

General leaf structure

A dicotyledonous leaf, like that of the bean or pea, is shown in *Fig. 2*. The upper and lower surfaces are protected by an **epidermis** of closely packed cells, coated with a **waxy cuticle** to minimize desiccation. **Leaf hairs** or **trichomes** may also project from the epidermis, which lessen air movement across the leaf (and therefore water loss). Beneath the epidermis lies the **palisade mesophyll**, normally one or two layers of elongated cells orientated perpendicular to the epidermis with many chloroplasts. Beneath this lies more photosynthetic tissue, the **spongy mesophyll**, surrounded by many air spaces, beneath which lies the **lower epidermis**. Carbon dioxide required by the leaf enters the leaf gas spaces by way of **stomata** (singular **stoma**), pores in the epidermis which are regulated by specialist epidermal cells called **guard cells** (Topic I2). The stomata lead to a cavity, the **substomatal cavity**, which connects with the gas spaces of the mesophyll.

Other types of leaf

Some species such as corn (maize; *Zea mays* L.) that show **C4 photosynthesis** (Topic J3), have a leaf structure in which a ring of **bundle sheath cells** surrounds the vascular bundle with mesophyll cells radiating from it in a **ring** (**Krantz [wreath] anatomy**; *Fig. 3*). These leaves have one type of mesophyll cell surrounding the bundle sheath with gas spaces beneath the stomata. Some **succulent** species that are adapted to drought have highly thickened, fleshy leaves that store water, a low surface area and thick cuticle that minimizes water loss. Frequently they only open their stomata at night (Topic J3). The needles of pines and other conifers have a small surface area, sunken stomata and a thick layer of protective tissue, the **hypodermis** just beneath the epidermis (*Fig. 4*), together with a protective layer (the **endodermis**) surrounding the vascular tissue. Other leaf adaptations to drought include having more stomata on the surface less exposed to desiccation and folds and tube-like structures that minimize air movement across leaf surfaces.

Leaves may be reduced to spines, as in cacti, or lost altogether in some plants in which the stem is the most important photosynthetic organ. A few other plants have outgrowths from the petiole or main stem that resemble leaves and act like them. The acacias of Australia, for instance, have flattened petioles but no lamina, while the butchers' broom of Europe has no leaves, but flattened stem outgrowths that bear flowers. **Modified leaves** also have a number of important roles in the plant, for instance as storage tissue in the **fleshy scales** of bulbs, as the **protective scales** of buds or as **tendrils**, which give support to climbing plants.

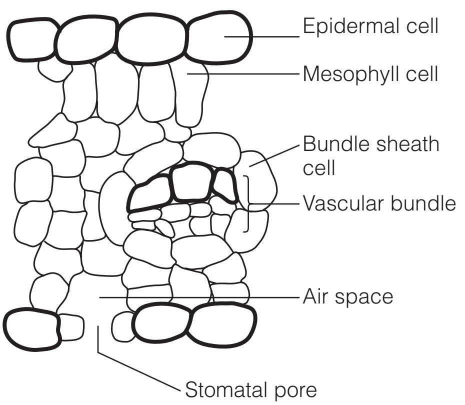


Fig. 3. A transverse section of the leaf of a species showing Krantz anatomy. Note the absence of spongy mesophyll and the arrangement of mesophyll around bundle sheath cells forming a wreath-like structure.

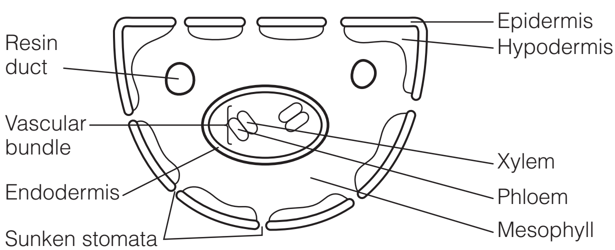


Fig. 4. A transverse section of a pine needle, which shows adaptation to drought. Note the low surface area, the protective hypodermis below the epidermis, sunken stomata and the endodermis surrounding the central vascular bundle.