Chapter 1

Plant life: a primer

1.1 An introduction to plant biology

We begin our investigation of how genes, proteins, metabolites and environmental signals interact in living plants by recognizing that readers may approach this subject from different backgrounds. To provide a common knowledge base, we have developed this chapter as a plant biology primer. For readers well versed in the evolution, development, anatomy and morphology of plants, this chapter will review familiar topics. For those not yet exposed to these disciplines, the chapter provides grounding in the biology of whole plants and introduces the plant life cycle on which this textbook is structured. Many of the terms and concepts introduced here will be revisited as later chapters delve into the processes and mechanisms that underlie each stage of plant life, describing the intricate network of cellular, molecular, biochemical and physiological events through which plants make life on land possible. We will be discussing the types of evidence used to develop modern classification schemes, and the evolutionary history and relationships among the groups of green plants alive today. These will provide a basis for the discussion of the fundamentals of plant anatomy, development and reproductive biology.

1.2 Plant systematics

What makes a plant a plant? This seemingly simple question has challenged biologists for centuries. The science of systematics seeks to identify organisms and order them in hierarchical classification schemes based on their evolutionary (phylogenetic) relationships. The levels of classification range from the domain, the most inclusive group, to the species, the most exclusive group (Table 1.1). Such schemes have predictive value, making it easier to distinguish individual organisms by name and to recognize groups of close or distant relatives. Members of a group of species at any level of classification are sometimes referred to as a taxon (plural: taxa), and the science of classification is called taxonomy.

1.2.1 Each species has a unique scientific name that reflects its phylogeny

The scientific name of a plant includes its genus and species names. Carolus Linnaeus developed the genus/species binomial in 1753 as a shorthand version of the long polynomial name he gave each plant in his major taxonomic work, Species Plantarum. Linnaeus’s polynomials have fallen out of use, but the binomial system has survived as the cornerstone of all biological classification schemes.

Latin binomials are italicized, with the first letter of the genus name capitalized and the first letter of the species epithet in lower case. Often a specific attribution is added to the binomial. In the case of domesticated barley, Hordeum vulgare, this binomial was used first by Linnaeus, so the abbreviation ‘L.’ is appended in Roman typeface: Hordeum vulgare L. (Figure 1.1). After first use of the full binomial in a document or in a discussion of
### Table 1.1

The ranks used in the classification of plants, as illustrated for domesticated barley (*Hordeum vulgare*).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Domain</td>
<td>Eukarya</td>
</tr>
<tr>
<td>Kingdom</td>
<td>Viridiplantae (green plant)</td>
</tr>
<tr>
<td>Phylum (Division)</td>
<td>Magnoliophyta (flowering plant)</td>
</tr>
<tr>
<td>Class</td>
<td>Liliopsida (monocot)</td>
</tr>
<tr>
<td>Order</td>
<td>Poales</td>
</tr>
<tr>
<td>Family</td>
<td>Poaceae (grass family)</td>
</tr>
<tr>
<td>Genus</td>
<td><em>Hordeum</em> (barley)</td>
</tr>
<tr>
<td>Species</td>
<td><em>vulgare</em></td>
</tr>
</tbody>
</table>

Figure 1.1 The Latin binomial for this barley plant is *Hordeum vulgare* L. 'Galena'.

several barley species, the shortened form *H. vulgare* can be used.

The value of coupling the binomial system to phylogeny-based classification becomes apparent when considering the muddle of common botanical names. Take 'beans', for example. The many plants that are referred to as beans do not belong to the same genus, the same family or even the same order (Figure 1.2). The common edible beans you might find on a dinner plate belong to the bean family, Fabaceae, but the plant that produces the castor bean is *Ricinus communis* in the family Euphorbiaceae, and the coffee bean comes from *Coffea arabica*, a member of the Rubiaceae. To make the situation more complex, the beans in the family Fabaceae belong to a number of different genera and often have many different common names. One example is *Phaseolus vulgaris*, a single species whose cultivated varieties produce adzuki, dry, French, green, pinto, runner, snap and wax beans. Other species in the same genus include lima beans (*P. limensis*) and butter beans (*P. lunatus*). Another genus in Fabaceae, *Vicia*, has 160 separate species, including *Vicia faba*. As you might guess from the specific epithet *faba*, *Vicia faba* is the fava bean, but this species is also called the broad, English, field, horse, pigeon, tick or Windsor bean (Figure 1.2).

Plant scientists often encounter the term *cultivar*, which is used to describe the cultivated varieties that plant breeders produce from wild species. When the cultivar is known, it is denoted by single quotation marks and/or the abbreviation ‘cv.’ and follows the Latin binomial. Cultivar names are in a language other than Latin. They are not italicized, and first letter(s) are capitalized: *Hordeum vulgare* L. ‘Golden Promise’ is the current convention, but the forms *Hordeum vulgare* L. cv. ‘Golden Promise’ and *Hordeum vulgare* L. cv. Golden Promise have also been used.

**Key points**

Common names have limited usefulness in identifying plants. The broad bean in the UK is the fava bean in the USA, but this plant is also referred to as the faba, field or horse bean, among other names. Plant biologists use the Latin binomial system devised by Linnaeus to describe species and the binomial for fava bean is *Vicia faba*. Binomials are written with a strict set of rules. The first epithet, as in *Vicia*, is the organism’s genus and the second, *faba*, is the species. The binomial is often followed by an abbreviated attribution that identifies the person who gave the organism its binomial. In the case of *V. faba*, it is followed by L., identifying Linnaeus as the authority. Binomials are abbreviated when they are used repetitively as above, *V. faba*, the genus denoted by the first letter followed by the full species name. Binomials are also displayed in italic font whereas the authority is typed plain font.

1.2.2 Modern classification schemes attempt to establish evolutionary relationships

Classification schemes based on phylogeny attempt to construct taxa that are monophyletic, that is, groups that include an ancestral species, all of its descendants and only its descendants. Modern methods of phylogenetic analysis are known as cladistics, a term derived from the word clade. A clade is a monophyletic taxon. In this chapter we will be using evolutionary trees called cladograms (Figure 1.3) to illustrate current hypotheses about the evolutionary history of plants.
Figure 1.2 The common name ‘bean’ is used to refer to plants belonging to many different families and genera. These images show four ‘beans’ belonging to three different families and four different genera. This illustrates the importance of using the Latin binomial when identifying plants. (A) French bean (Fabaceae, *Phaseolus vulgaris*). (B) Fava bean (Fabaceae, *Vicia faba*). (C) Castor bean (Euphorbiaceae, *Ricinus communis*). (D) Coffee bean (Rubiaceae, *Coffea arabica*).

Figure 1.3 Cladogram illustrating the evolution of green plants.
To construct cladograms, systematists and evolutionary biologists use morphological, anatomical and metabolic traits as well as biochemical and molecular-genetic data. The tree is rooted using an **outgroup**, a relative of the taxon under investigation (the **ingroup**). The ingroup and the outgroup share certain **primitive traits**; members of the ingroup have acquired new **derived traits** that distinguish them from the outgroup. For example, in the cladogram in Figure 1.3, red algae are the outgroup for the green plant clade. Red algae and green plants share certain primitive traits, such as having cell walls composed of cellulose (see Chapter 4) and chloroplasts enclosed by two membranes. Chloroplasts of green plants, unlike those of red algae, contain both chlorophyll a and chlorophyll b; the presence of chlorophyll b is a major character that separates green plants from red algae. The remainder of the cladogram is constructed in a similar fashion. At each branch point, the clade above the branch point has derived traits that separate it from the taxa below the branch.

### 1.3 The origin of land plants

To understand the evolution of the land plants, it is useful to look at their evolutionary origins. Life originated on Earth more than 3.5 bybp (billion years before present) and it is believed that the fundamental design of the photosynthetic apparatus was established early in evolution. Chloroplasts, the subcellular structures that carry out photosynthesis in plants, are derived from photosynthetic bacteria (cyanobacteria) that, according to most estimates, entered into an endosymbiotic association with early animal-like unicellular organisms (protozoa) around 1.5 bybp. The primary endosymbiotic event soon gave rise to two evolutionary lineages, the so-called glaucophytes (a small group of alga-like unicellular freshwater organisms) and the red algal/green plant branch. Other photosynthetic protists acquired their chloroplasts by secondary endosymbiosis during which they engulfed unicellular red or green algae. Here we examine the further diversification of the green plant group leading to the land plants, the subject of this book.

#### 1.3.1 The green plant clade, viridophytes, includes the green algae and land plants

The ancestors of land plants are widely believed to be the green algae. These two groups make up the green plant clade, the **viridoplantae**. The viridophytes are photosynthetic organisms whose chloroplasts are enclosed by two membranes, contain chlorophylls a and b and store starch. Cytological and molecular data support the division of the viridophytes into two clades that diverged more than 1 bybp: the **chlorophytes**, composed of most green algae, and the **streptophytes**, which include **charophycean green algae**, such as *Chara* and *Coleochaete* (Figure 1.4), and the **land plants**. Land plants, the **embryophytes**, have multicellular reproductive organs and produce embryos that are protected and nourished by the parent plant.

#### 1.3.2 Unlike their green algal ancestors, embryophytes have evolved adaptations to life on land

Evolution of land plants has been driven by problems associated with living on dry land. Plants require carbon dioxide, water and light for photosynthesis. In addition, they need access to O₂ and to inorganic ions containing a number of different elements, including nitrogen, phosphorus, potassium, sulfur, etc. (see Chapter 13). Green algal ancestors of land plants were relatively simple, aquatic organisms (Figure 1.5). To survive and thrive on land, plants encountered several challenges. Organisms living on land are exposed to dry air and therefore need waterproofing layers and specialized pores, **stomata**, to allow uptake of carbon dioxide. Air does not provide buoyant support; this led to the evolution of support tissues to keep plants upright. **Resources** essential for plant growth are usually spatially separated: light is above ground and water and minerals are in the soil. This led to the evolution of specialized aerial **photosynthetic organs** (leaves), **underground organs** (roots) specialized for uptake of water and inorganic ions and **connecting organs** (stems) with efficient transport systems to move sugar from the photosynthetic tissues to the roots and water and minerals upwards from the soil to the leaves.

The transition from aquatic living to life on land also impacted on reproduction. To understand this impact, we need to look at sexual reproduction in plants. The pattern of sexual reproduction in land plants is quite different from that of animals (Figure 1.6). In animals, including humans, the adult body is made of **diploid** (2n) cells. Meiosis produces **haploid** (n) **gametes**, eggs and sperm; these are the only haploid cells in the animal life cycle. Egg and sperm fuse at fertilization to produce a diploid zygote that gives rise to the next diploid generation. In contrast, sexual reproduction in land plants involves an **alternation** between a diploid
Figure 1.4 Representative green algae: (A) Ulva, (B) Chlamydomonas, (C) Nitella and (D) Coleochaete.

Figure 1.5 Comparison of an aquatic green alga and a terrestrial vascular plant.
**Part I** Origins

**Figure 1.6** Comparison of generalized life cycles of plants and animals. (A) The animal life cycle features one multicellular generation, which is diploid. The only haploid cells are the gametes produced by meiosis. (B) The plant life cycle has an alternation of multicellular generations; one is haploid, the other diploid. Gametes are produced by the haploid generation via mitosis. Meiosis in the diploid generation generates spores that germinate to yield the haploid generation.

**Key points** Evolutionary trees or cladograms are used to establish evolutionary relationships among groups of organisms. The goal of this branch of biology, called cladistics, is to identify ancestral organisms and all of their descendants using key features that distinguish them from all other organisms. Organisms belonging to a unique group are referred to as a clade or a taxon. Plants can be divided into two distinct clades, ancestral green algae and land plants. Land plants are distinguished from algae by retention of the fertilized egg and protection and nourishment of the embryo by the parent plant. The retention of the embryo was among several features that allowed the transition from an aquatic existence to life on land. Among the other key features that evolved were a protective outer waxy layer that limited evaporation of water, closable pores for gas exchange, water transporting tissue and mechanisms of reproduction that eventually eliminated the need for liquid water.

**1.4 Bryophytes**

The bryophytes are the most primitive group of embryophytes. This group is paraphyletic (i.e. its members do not share a common ancestor); it includes three monophyletic clades, the hornworts, liverworts and mosses (see Figures 1.3 and 1.7). About 24,000 bryophyte species exist today. The first bryophytes are
thought to have diverged from the vascular plant lineage more than 450 million years before present (mybp).

**Key points** Reproduction in plants is fundamentally different from that in animals. While in animals eggs and sperm are produced by meiosis, plants produce eggs and sperm by mitosis. Haploid spores are produced by meiosis by the diploid spore-making sporophyte plants. Spores germinate to produce a haploid gamete-making plant called the gametophyte that produces eggs and sperm by mitosis. This so-called alternation of generations between sporophyte and gametophyte is well illustrated in ferns. Large leafy ferns are sporophytes and spores produced by meiosis are found on the underside of leaves. Spores are shed and germinate to produce a gametophyte, rarely more that a few millimeters in diameter. Eggs and motile sperm are produced by the gametophyte plant and after fertilization the resulting zygote grows to the mature sporophyte plant.

1.4.1 Bryophytes have adapted to a range of environments and show a limited degree of differentiation into tissues and organs

Bryophytes are usually associated with damp, even wet, environments such as acidic peat bogs in which *Sphagnum* moss is abundant, but they also occur in environments that are seasonally dry and hot. For example, mosses are widely distributed on surfaces such as roofing tiles, slate and rocks. In these environments, they survive dry periods in a desiccated state and rehydrate and grow when moisture is available. Bryophytes are also abundant above the tree line and cover large areas in the Arctic regions.

The photosynthetic plants that we recognize as mosses, liverworts or hornworts, are haploid gametophytes (Figure 1.7). In hornworts and many liverwort species, the gametophyte takes the form of a thallus, a flattened body that hugs the ground. On its underside it produces rhizoids, elongate single cells that anchor the gametophyte to the substrate. The gametophytes of leafy liverworts and mosses are differentiated into leaf-like and stem-like organs (Figures 1.7 and 1.8) that may be covered in a cuticle. Often, the central part of the moss ‘stem’ contains elongate cells that are thought to participate in the transport of water and solutes, but these cells are different in structure and origin to the cells of the water-conducting tissue of vascular plants. Multicellular, filamentous rhizoids anchor the moss gametophyte to its substrate. Diploid sporophytes are less conspicuous and are nutritionally dependent on gametophytes.

1.4.2 Gametophytes dominate the bryophyte life cycle

The life cycle of a typical moss is shown in Figure 1.8. The gametophyte produces gametes in multicellular gametangia. The egg remains within the female gametangium (*archegonium*); biflagellate sperm are released from the male gametangium (*antheridium*) and swim through a film of water to the egg. **Fertilization** takes place in the archegonium.

**Figure 1.7** Representative bryophytes: (A) moss, (B) liverwort and (C) hornwort.
The resulting diploid zygote divides in situ, to produce a diploid embryo. The embryo develops into the sporophyte that remains attached to and dependent on the gametophyte.

A mature sporophyte has a stalk (seta) and sporangium (capsule). In the stalk of the sporophyte, a central cylinder of differentiated cells may be the functional progenitor of the vascular system of vascular plants; stomata may also be present in the sporophyte. Within the sporangium, diploid cells divide by meiosis to produce haploid spores. Bryophyte spores are enclosed in a thick cell wall that contains sporopollenin, a polymer known to reduce water loss and resist degradation. Spores are dispersed by wind. When spores germinate, they develop into a new gametophyte generation.
Key points  Bryophytes are the most primitive land plants. Reproduction in bryophytes requires liquid water for sperm to reach the egg. The resulting zygote develops into an embryo surrounded by maternal tissue. The sporophyte remains attached to and is nourished by the female gametophyte. Haploid spores, produced by meiosis, are wind dispersed. The free-living gametophytes of bryophytes lack many adaptations for living on dry land, including a waterproof cuticle and a well-developed vascular system, but are thought to be the progenitors of vascular plants.

1.4.3 Many features of bryophytes suggest a link to the vascular plants

Sporophytes of bryophytes show several adaptations to life on dry land, including the presence of cuticle, stomates and transport cells and the production of desiccation-resistant, wind-dispersed spores. However, because they are dependent on gametophytes for nutrition, sporophytes are limited to environments that are at least seasonally wet, where gametophytes can thrive. While gametophytes have some cuticle, their tissues are subject to desiccation; absorption of water and minerals takes place over the surface of the whole plant. They lack stiffening tissue and so remain relatively small. Sexual reproduction requires a film of water through which motile sperm can swim to non-motile eggs. However, the presence of multicellular sex organs and the fact that the diploid embryo is protected and nourished by the gametophyte represent adaptations to life on land.

1.5 Vascular plants

Fossil evidence indicates that the first vascular plants (tracheophytes) were simple, dichotomously branched organisms about 5–10 cm in height. In the earliest vascular plants, the gametophyte and sporophyte are believed to have been free-living and approximately equal in size. These early land plants had specialized vascular tissue for conducting water, sugar and minerals (see Sections 1.8.2–1.8.4). Morphological and molecular evidence supports the division of living vascular plants into three clades: lycophytes, ferns and allied taxa (monilophytes) and seed plants (lignophytes) (see Figure 1.3). Within the vascular plant clade, we shall see a progressive reduction in the size and life span of the gametophyte generation and an increase in the size and importance of the sporophyte generation. Plants that are recognized as ferns, pine trees and flowering plants are diploid sporophytes. We will first examine the vascular spore plants, the lycophytes and the monilophytes. In these two groups, although sporophytes are more prominent, both sporophytes and gametophytes are free-living, independent plants. In both groups, sporophytes produce spores that are wind dispersed.

Key points  Vascular plants are characterized by the presence of a well-developed transport system, epidermis with a cuticle and stomates on leaves and stems, and their sporophytes are well adapted to life on land. Three clades of vascular plants are extant, the lycophytes, ferns and allied taxa, and seed plants. Lycophytes and ferns and their allies all have alternation of free-living sporophyte and gametophyte generations, with sporophytes being the dominant generation and best adapted to land. Their gametophytes are much reduced in size and the motile sperm they produce require water for fertilization. Extant lycophytes such as the quillworts and Selaginella are relatively small and inconspicuous and live in well-watered environments. In the Carboniferous period, members of this clade formed forests with trees in excess of 30 m in height that gave rise to today’s coal deposits. Ferns were also abundant in the Carboniferous; these plants were larger than extant ferns.

1.5.1 Lycophytes were among the first tracheophytes to evolve

Extant lycophytes form a distinct clade that split from other tracheophytes about 400 mybp. Today they are few in number, about 1200 species, but during the Carboniferous period, diverse lycophytes dominated the landscape and gave rise to coal deposits. Extinct members of this clade include large trees that produced woody trunks by processes similar to those found in woody seed plants. Living lycophytes are represented by the club mosses (e.g. Lycopodium), the spike mosses,
1.5.2 Ferns, horsetails and whisk ferns constitute a single monophyletic clade, the monilophytes

The monilophytes, which arose more than 360 mybp, include the ferns (Ophioglossaceae, Marattiales and Polypodiales), horsetails (Equisetales) and whisk ferns (Psilotaceae) (Figure 1.10). Along with the lycophytes, the ferns and allied groups contributed to the formation of coal during the Carboniferous period. Today, although they have limited economic value, they play important ecological roles. Ferns are numerous (exceeding 11 000 species) and abundant, especially in the tropics.

The phylogenetic relationships among monilophytes have been inferred from gene sequences. When only morphological characters were available for comparison, systematists did not consider these plants monophyletic. For example, the leafless, rootless whisk ferns (e.g. *Psilotum*) were thought to be more primitive than the lycophytes, but molecular phylogeny places them firmly in the monilophyte clade.

1.5.3 Although adapted to land, ferns require water for reproduction

Although some fern orders (e.g. Salviniales) are aquatic, most ferns are terrestrial. As in lycophytes, the fern life cycle includes a large sporophyte generation and an inconspicuous, though independent, gametophyte (Figure 1.11). Fern sporophytes are well adapted to land; their above-ground parts are covered by a cuticle and an epidermis in which stomata are embedded. Leaves are generally large, multiveined and may be highly divided. They are often the only above-ground part of the fern plant. Most ferns have a horizontal underground stem (a rhizome) and a complex root system. Fern sporophytes produce wind-dispersed, haploid spores in sporangia borne on the undersides of leaves. Spores germinate to form haploid gametophytes that may have male and female gametangia on the same plant or on separate gametophytes. In a few species, sporophytes produce two types of sporangia: megasporangia that make large spores (megaspores) and microsporangia that make small spores (microspores). Megaspores develop into female gametophytes and microspores develop into male gametophytes.

Fern gametophytes are photosynthetic. They are small, rarely more than 1 cm in diameter, and usually only one to two cells thick. Gametophytes lack cuticle, vascular tissue and true organs; simple unicellular rhizoids anchor them to the substrate. They can only survive in damp areas. Gametophytes produce eggs in archegonia and flagellated sperm in antheridia. The sperm swim through a layer of water to reach the egg.
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After fertilization, the diploid zygote develops into an embryonic sporophyte within an archegonium of the gametophyte. As the young sporophyte produces leaves, stems and roots, it overgrows the parent gametophyte.

Sporophytes of vascular spore-producing plants (lycophytes, ferns and allied groups) are well adapted to life on dry land. However, their gametophytes remain tied to wet areas by their anatomy and the fact that fertilization requires water. Because sporophytes begin life attached to gametophytes, they must start life in moist areas. The problem of a vulnerable gametophyte was overcome when the seed plants evolved.

Figure 1.10 Diverse morphologies of some members of the fern clade (monilophytes), which do not demonstrate their membership in a monophyletic clade. These relationships were established using DNA sequence data. (A) *Equisetum* (horsetails). (B) *Psilotum* (whisk fern). (C, D) The true ferns: (C) *Polystichum* and (D) *Cyathea*, a tree fern.

### 1.5.4 Seed plants are successful conquerors of land

Living seed plants are divided two monophyletic clades, the **gymnosperms**, including five major lineages—the cycads, the pine family, other conifers, gnetophytes and **Ginkgo**—and the **angiosperms** (the flowering plants) (see Figure 1.3). The gymnosperm lineages contain more than 800 extant species. Flower-bearing angiosperms are by far the largest seed plant lineage, including more than 254,000 species. This number is probably an underestimate because it is likely that many members of this clade await discovery.

Seed plants provide many key resources, including food, lumber, fiber and fuel. Given their significance in our lives and their centrality to this book, we will describe in detail their reproduction, structure and development. First, we will examine the phylogeny and reproductive biology of gymnosperms and angiosperms separately. Later, in Sections 1.7–1.10, we discuss the anatomy and development of angiosperms noting similarities and differences with gymnosperms.

### 1.5.5 Seeds encase the embryo and its food, facilitating dispersal of the new sporophyte generation

Seed plant sporophytes produce two kinds of sporangia: **ovules** (*megasporangia*) and **pollen sacks** (*microsporangia*). Spores produced in these sporangia are not released, but divide in situ to produce gametophytes. Ovules enclose female gametophytes; pollen sacks contain male gametophytes, called **pollen**.
Three major reproductive advances in adapting to life on land are found in seed plants. First, haploid gametophytes are reduced in size and are protected within sporangia on the parent sporophyte. Second, seed plants no longer require a film of water for fertilization. The male gametophyte, a pollen grain, develops a protective coat and is delivered to the vicinity of the female gametophyte by wind or by animal pollinators.
Finally, a new dispersal stage, the seed has evolved. A seed, with its protective seed coat, contains a new sporophyte with a source of food. We shall see below how each of these features is incorporated into the life cycles of first a gymnosperm and then an angiosperm.

Key points
Seed plants contain two distinct clades, gymnosperms and angiosperms. Seed plants successfully colonized land because a mode of reproduction evolved that made sexual reproduction independent of liquid water. They were also successful because the seed was relatively long-lived and provided seedlings with stored food for survival after germination. The sporophyte is the dominant part of the seed plant life cycle. The gametophytes are retained, protected and nourished by the sporophyte. Pollen evolved as the vehicle to deliver sperm to the egg without a film of water.

1.6 Gymnosperm phylogeny and reproduction

The term gymnosperm is derived from Greek: gymnos, bare or naked, and sperm, seed. The name refers to the gymnosperm seed, which is not enclosed in a protective structure as it is in the angiosperm ovary (ang(os) = vessel (Greek)). Gymnosperms were the dominant land plants in the Cretaceous and Jurassic periods, the age of dinosaurs. There are about 800 species of gymnosperms in the present-day flora.

1.6.1 Gymnosperm phylogeny reveals five lineages

Gymnosperms arose more than 320 mybp. Previously, Gymnosperms had been classified into four groups: the cycads; the ginkgophytes, containing one extant species Ginkgo biloba; the gnetophytes, including Ephedra, Gnetum and Welwitschia; and the conifers (Figure 1.12A–D). Analyses of DNA sequences of chloroplast, mitochondrial and nuclear genes, however, have shown that the conifers are divided into two lineages, the Pinaceae (pine family) and the rest of the conifers (see Figure 1.3). Pinaceae consists of nine genera including Pinus (pine), Abies (fir), Picea (spruce), Cedrus (cedar), Tsuga (hemlock) and Pseudotsuga (Douglas fir). The second conifer lineage includes five families: Araucariaceae (Araucaria family), Cephalotaxaceae (plum yew family), Podocarpaceae (Podocarpus family), Taxaceae (yew family) and Cupressaceae (Cypress family, including Sequoia, Sequoiadendron (Figure 1.12E), Chamaecyparis, Thuja and Juniperus.

1.6.2 Conifers constitute an important natural resource

The best-known and most diverse gymnosperms are found in the pine and other conifer lineages. Sporophytes in these lineages are among the largest and oldest living organisms in the biosphere. They are well adapted for life on dry land. Many have needle-like leaves that resist water loss. The needles are circular in cross section giving them a low surface to volume ratio; the epidermis is covered by a thick cuticle. Pines and other conifers produce large woody stems (see Section 1.10). The coastal redwood (Sequoia sempervirens) can exceed 100 m in height and the giant sequoia (Sequoiadendron giganteum) 8 m in diameter. Some bristlecone pine trees (Pinus longaeva) have lived to an age of more than 4900 years.

In contrast to the other gymnosperm lineages, the pine family and other conifers have great economic value and broad ecological significance. They provide lumber for building materials and pulp for paper. The northern coniferous forest (taiga) is among Earth’s largest terrestrial biomes, and pines and other conifer species are also common in many temperate forests at lower latitudes. Given their significance as a commodity and as habitat, we focus our discussion of gymnosperm reproduction in the genus Pinus.

1.6.3 Sporangia and gametophytes of pines and other conifers are produced in cones

The life cycle of Pinus is illustrated in Figure 1.13. As is the case in most gymnosperms, ovules are produced in seed cones (female) and pollen sacs are produced in pollen cones (male) (Figure 1.14). The pollen cone consists of cone scales, each of which bears two pollen sacs. Inside a pollen sac are many diploid microspore mother cells that undergo meiosis, forming haploid...
microspores. Each microspore divides by mitosis to produce a male gametophyte (pollen grain). The mature pollen grain is enclosed in a thick cell wall; it has a generative cell that will give rise to the sperm, a tube cell that functions in sperm delivery, and two prothallial cells that typically degenerate. When mature, pollen grains are released from the male cone and are dispersed by the wind to female cones.

In the female cone, ovules are produced on ovuliferous scales; each scale bears two ovules. An ovule is enclosed in a protective integument that has an opening at one end that allows the pollen tube to enter. A cell at the center of the ovule, a megaspore mother cell, divides by meiosis to produce four haploid megaspores, three of which degenerate. The remaining megaspore divides by mitosis to produce a female gametophyte. The female gametophyte is retained within and nourished by the ovule.

1.6.4 Pine reproduction is characterized by a long delay between pollination and fertilization

In pine, pollination—the transfer of pollen from a male cone to an ovule in a female cone—occurs a few weeks before megaspores are formed within the ovule. The outer surface of the female cone exudes sticky secretions between the cone scales called pollination droplets. Wind-borne pollen grains stick to the droplets; as these dry, they draw the pollen grains toward the ovules. About 3 months after pollination, the pollen grains germinate and produce pollen tubes that will carry sperm to the female gametophyte within the ovule. It can take up to a year for the pollen tube to reach the female gametophyte.
Figure 1.13  Life cycle of a pine (*Pinus* sp.). (1) Male and female cones have scales bearing two sporangia, (2) pollen sacs or microsporangia in the male and ovules or megasporangia in the female. (3) In each pollen sac many microspore mother cells divide by meiosis to produce haploid microspores that develop into pollen grains (male gametophytes). In the female cone, in each ovule one megaspore mother cell divides by meiosis to produce a single megaspore which develops into a female gametophyte that bears archegonia with eggs. (4) Pollen is dispersed by wind and lands on an ovule within a female cone and germinates to produce a pollen tube containing two sperm, one of which will fertilize the egg. (5) The resulting diploid zygote develops into an embryo. (6) A single female cone scale bears two ovules, each of which contains an embryo sporophyte and develops into (7) a winged seed. (8) The seeds germinate to produce a new seedling sporophyte. Reproduction in *Pinus* from the initiation of cone development to the release of seeds takes about 3 years.

Meanwhile, shortly after pollination, female gametophyte development begins. After 6 months to 1 year, a mature female gametophyte produces several archegonia, each containing one egg. At about this time the pollen tube reaches the female gametophyte. Its generative cell divides once to produce a sterile cell and a spermatogenous cell. As the pollen tube approaches an archegonium, the spermatogenous cell divides to produce two sperm that lack flagella. The pollen tube fuses with the plasma membrane of the egg cell and discharges both sperm into the egg cytoplasm. One sperm fertilizes the egg, producing a diploid zygote, and the other degenerates. Many pollen tubes may grow into a single ovule, and several eggs can be fertilized. Typically, only one zygote develops into an embryo.

1.6.5 Pine seeds contain both diploid and haploid tissues

After fertilization, as embryo development proceeds, the inner tissue of the ovule may increase in size. The
enveloping integument becomes the seed coat. The mature pine seed (Figure 1.15) contains tissues from three genetically distinct generations: (1) the seed coat, from the parent sporophyte, that forms a hard protective layer around the seed; (2) the haploid female gametophyte that contains stored food that will be used to nourish the embryo; and (3) the diploid embryo. Edible pine nuts found in grocery stores are pine female gametophytes plus embedded embryos. Seeds of pines and other conifers are often winged to aid in their dispersal.

1.7 Angiosperm phylogeny and reproduction

An extensive fossil record indicates that flowering plants arose more than 140 mybp. Traditionally, the angiosperms were divided into two clearly recognizable groups, the eudicots and monocots. Most of the eudicots have two cotyledons (seed leaves), broad leaves with branched venation, and a taproot; many eudicots can form wood. The monocots have one
Key points The gymnosperms are defined by the presence of an ovule that is not enclosed within an ovary as is the case in angiosperms. The female gametophyte of *Pinus* is located within the ovule located on the surface of a female cone scale. Meiosis in the ovule gives rise to a megaspore that divides by mitosis to produce a haploid female gametophyte. Pollen develops from microspores that are the product of meiosis in male cones. In *Pinus* each pollen grain is a male gametophyte and has four cells. Pollen is wind dispersed in gymnosperms and is produced in vast amounts. Pollen grains land on the surface of mature female cones and are drawn into the cone by a drying pollination droplet. The pollen grain produces a pollen tube which grows through the ovule to deliver non-motile sperm to the female gametophyte. The pollen tube fuses with the egg cell membrane, discharging the sperm, and fertilization ensues. The zygote develops into an embryo in situ. Outer layers of the ovule form the seed coat enclosing the embryo and female gametophyte tissue which functions as a food reserve for the seedling.

cotyledon and narrow leaves with parallel venation; they generally lack wood.

More recent phylogenetic analyses, especially those incorporating data from morphology and gene sequences, provide a more complex view of angiosperm phylogeny. Figure 1.16 shows how angiosperms can be divided into a number of major groups based on gene sequences and the number of pores in the pollen cell wall.

1.7.1 The flower is the defining feature of angiosperms

Flowers are found only in angiosperms. The flower contains the reproductive organs of the angiosperm sporophyte: ovules and pollen sacs and associated sterile organs. A complete flower consists of four whorls (concentric rings) of organs (Figure 1.17). The sepals make up the outermost whorl, known also as the calyx; sepals are usually green and protect the internal floral organs in a flower bud. Moving inward, the next whorl, the corolla, is made up of petals which are often brightly colored and may serve to attract animal pollinators. In contrast to wind pollination, the use of animal pollinators allows more precise targeting of pollen delivery and allows pollen to be transported over longer distances. Stamens form the next whorl, the androecium. Each stamen consists of a stalk-like filament and an anther made up of pollen sacs. The innermost whorl, the gynoecium consists of one to many carpels. Each vase-shaped carpel has a stigma upon which pollen lands, a neck-like style through which pollen tubes grow, and an ovary that contains one to many ovules. The carpel is unique to angiosperms; it protects the ovules and, as we shall see below, develops into a fruit.
integuments with a small opening, the micropyle, at one end. Within the ovule, one cell divides by meiosis to produce four haploid megaspores of which three degenerate. The surviving megaspore divides by mitosis to produce a female gametophyte, the embryo sac. Three rounds of mitosis produce seven cells: three uninucleate cells at each end of the gametophyte and one large central cell with two polar nuclei. Of the trio of cells at the micropylar end of the embryo sac, the middle cell is the egg; the two adjacent cells are the synergids, one of which determines the point of entry of the pollen tube into the embryo sac. The three cells at the opposite end of the gametophyte are called the antipodals. The mature angiosperm female gametophyte has only seven cells in contrast to the female gametophyte of gymnosperms that typically has thousands.

1.7.3 Double fertilization in angiosperms leads to the formation of a diploid embryo and polyploid endosperm

Pollination occurs when pollen is transferred from a pollen sac to the stigma of a carpel. Mechanisms exist that prevent pollen germination or growth unless the pollen and stigma/style are compatible (see Chapter 16). When pollen germinates, it produces a pollen tube containing two sperm. The pollen tube grows down the style of the carpel carrying the two sperm near its tip. It enters an ovule through the micropyle. When it reaches the embryo sac, the pollen tube fuses with one of the synergid cells and releases the sperm. One sperm fuses with the egg to produce a diploid zygote. The second sperm fuses with the two polar nuclei and forms a triploid, primary endosperm cell. These events are called double fertilization; the second fertilization event is unique to angiosperms.

After double fertilization, the zygote divides to produce the new embryo and the primary endosperm cell divides to form a unique nutritive tissue, the endosperm. The endosperm of angiosperm seeds takes the place of the large, multicellular female gametophyte that nourishes the developing embryo in all other embryophytes. Development of the embryo and endosperm starts almost immediately after fertilization. The patterns of early embryonic development, embryogeny, are strikingly similar in all angiosperms (Figure 1.19). The first division of the zygote is transverse and produces two cells, an apical cell that gives rise to most of the embryo and a basal cell that gives rise to part of the embryonic root apex and to the suspensor. Continued cell division in the embryo gives rise to a ball of cells referred to as the globular stage. During this
stage, tissue precursors begin to form. In primitive dicots and eudicots, cell division coupled with differing rates of cell expansion result in the formation of two cotyledons (seed leaves) that become evident at the heart stage of embryogeny. The shoot apical meristem arises in the notch between the two developing cotyledons. In monocots, a single cotyledon is formed. In this case, the shoot apical meristem forms on one side of the embryo, near the base of the cotyledon (Figure 1.20). A mature embryo usually consists of an embryonic root, the radicle; one or two cotyledons; and an embryonic shoot axis, including a hypocotyl (hypo = below, cotyl = cotyledons), an epicotyl (epi = above) and a shoot apical bud. The embryos of cereals and grasses are more complex than those of most monocots and eudicots (see Chapter 6).
Endosperm development typically begins before embryogenesis starts. The primary endosperm cell may undergo many rounds of free-nuclear division in which cell walls are not laid down. Walls are eventually laid down between nuclei to form a fully cellularized tissue. In the coconut palm, cellularization is not completed until the time of seed germination. As a result, coconuts contain both cellularized, solid endosperm, known as copra, and the free-nuclear liquid endosperm familiar as coconut water (Figure 1.21). The mature angiosperm seed consists of an **embryo** enclosed by a protective coat,
the **testa**, derived from the outer tissues of the **ovule** (see Chapter 6). In some cases the mature seed contains endosperm while in other seeds the endosperm is consumed during the later stages of embryo development. In Chapter 6 we describe the structure and function of seed tissues in more detail and examine their roles in dormancy and germination.

### 1.7.4 In angiosperms, fruits promote seed dispersal

While seeds are maturing within the ovary, the ovary wall enlarges and develops into a **fruit**. Fruits are ripened carpels containing seeds and are unique to angiosperms. In some species with single-seeded fruits, e.g. cereal grains, the wall of the ovary fuses with the seed coat; therefore the grain is technically a fruit not a seed.

Fruits are usually modified to enhance seed dispersal (Figure 1.22). In fleshy fruits, such as tomatoes and cherries, the ovary develops into tasty flesh. These fruits attract animals that eat them and deposit the indigestible seeds at some distance from the parent plant. In other plants, such as maple and elm, the ovary wall develops into a wing that aids in wind dispersal of seeds. Some fruits have fluffy parachutes that float seeds in the wind. In cocklebur, the ovary wall produces hooks that snag onto fur and feathers allowing the fruit and its enclosed seeds to hitchhike on animals. In coconut, the ovary wall becomes buoyant allowing the fruit to float.

When environmental conditions are favorable, seeds germinate and a new sporophyte seedling begins to grow. The process of germination is discussed in detail in Chapter 6. Below we will examine the organization and structure of a seed plant sporophyte using angiosperms as an example. Then we will discuss the basic principles of how this plant increases in size and produces new organs throughout its life.

### 1.8 The seed plant body plan I. Epidermis, ground tissue and vascular system

The body plan in angiosperms and gymnosperms is based on three types of vegetative (non-reproductive)
Key points  Angiosperms were originally thought to consist of two major groups, dicots and monocots, but more recent analysis shows that angiosperms are made up of at least 15 different lineages. The evolution of the flower with a carpel enclosing ovules was a major step in the evolution of plants. In addition to protecting the ovules, the carpel develops into a fruit that enhances seed dispersal. Another major evolutionary advance in angiosperms was the formation of endosperm as a result of double fertilization. The gametophyte phase of the angiosperm life cycle is even more reduced than that found in gymnosperms. The female gametophyte consists of an embryo sac containing seven cells, one of which is an egg with two polar nuclei. Pollen is delivered to the stigma of the carpel; pollen germination and pollen tube growth down the style to the ovule begins immediately. The pollen tube carries two non-motile sperm and delivers them to the embryo sac. One sperm fuses with the embryo to produce a zygote and the other sperm fuses with two polar nuclei to give a triploid endosperm. Embryo and endosperm grow by mitotic divisions to produce the seed; the ovule forms a protective seed coat.

organs: roots, stems and leaves. All roots of a plant comprise its root system, while its stems and leaves make up its shoot system (Figure 1.23). Each organ is made up of three tissue systems: dermal, ground and vascular tissue systems. The arrangement of these tissue systems within a plant is shown in Figure 1.24. As we shall see below each tissue system has a different function and is made up of a number of different cell types (Table 1.2).

1.8.1 Epidermal tissue covers the outside of a plant while ground tissue makes up the bulk of a plant

The dermal tissue system, composed of epidermis, covers and protects the internal tissues of each organ. The epidermis of aerial organs secretes a waterproof layer called cuticle to slow water loss. In regions of the root that take up water and minerals, cuticle is absent, rather epidermal cells produce long tubular extensions called root hairs that increase the surface area available for uptake. The epidermis contains several specialized cell types including gland cells, hair cells (also called trichomes) and guard cells that surround the stomata, pores in the epidermis that allow gas exchange (Figures 1.25 and 1.26). In contrast to other epidermal cells, stomatal guard cells contain chloroplasts; in addition they have specialized wall thickenings that allow them to regulate the size of the stomatal pore. Two types of guard cells are found in plants, the dumbbell-shaped guard cells characteristic of grasses and palms, and the sausage-shaped guard cells found in most eudicots (see Figure 14.29). Both types of guard cell have differentially thickened cell walls. The role of guard cells in opening and closing stomata is discussed in more detail in Chapter 14.

The ground tissue system makes up most of the volume of a plant. Most of the metabolic activities of the plant occur in this tissue. It is largely composed of parenchyma cells (Figure 1.27) with thin flexible primary cell walls (see Chapter 4). They are relatively unspecialized and are involved in the production and storage of carbohydrate and other organic molecules. Collenchyma and sclerenchyma tissues can also be found in the ground tissue system (Figure 1.27). Collenchyma cells have primary cell walls with uneven
Figure 1.24 Arrangement of three tissue systems, vascular, ground and dermal, in a vascular plant in longitudinal and cross-section views. Shown are cross-sections of (A) a leaf, (B) a shoot and (C) a root.

Table 1.2 Tissue systems, tissues and cell types found in plant organs.

<table>
<thead>
<tr>
<th>Tissue systems</th>
<th>Tissues</th>
<th>Types of cells</th>
</tr>
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<tbody>
<tr>
<td>Dermal</td>
<td>Epidermis</td>
<td>Epidermal cells, guard cells, gland cells, hair cells</td>
</tr>
<tr>
<td>Ground</td>
<td>Ground tissue</td>
<td>Parenchyma cells</td>
</tr>
<tr>
<td></td>
<td>Sclerenchyma</td>
<td>Fibers, sclerids</td>
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<tr>
<td></td>
<td>Collenchyma</td>
<td>Collenchyma cells</td>
</tr>
<tr>
<td>Vascular</td>
<td>Xylem tissue</td>
<td>Tracheary elements (vessel elements and tracheids), fiber cells, parenchyma cells</td>
</tr>
<tr>
<td></td>
<td>Phloem tissue</td>
<td>Sieve tube elements (members), companion cells, fiber cells, parenchyma cells</td>
</tr>
</tbody>
</table>

Figure 1.25 Scanning electron micrographs of some of the cell types found in the dermal tissue system. (A) Gland cells that secrete oils. (B) Trichomes that may discourage predators or reflect excess light.

thickenings, usually at the corners of the cells. These cells usually occur in bundles, e.g. in the ribs of celery stalks, and provide flexible support to petioles and the main veins of leaves. Sclerenchyma cells—fibers and sclereids—have thick, highly lignified, secondary cell walls and may be dead at maturity. Sclereids, often called stone cells, are cube-shaped and tend to occur in clusters. They are best known for the gritty texture they give to fruits such as pears. Fibers are elongate cells, found individually or in groups, that add strength to tissues, providing rigid support.
Key points The body plan of seed plants is simple and composed of a shoot and root system. The shoot includes two organs, stems and leaves; roots are the organs of the root system. Each of these organs is made up of three primary tissue types, all derived from the root and shoot apical meristems. The apical meristem gives rise to dermal, ground and meristem tissue systems. Dermal tissue covering the entire plant is epidermis, a tissue specialized for protection and water conservation in stems and leaves and for water uptake in young roots. Epidermis encloses ground tissue within which vascular tissue is embedded. Ground tissue is comprised of primarily parenchyma that has different functions depending on its location in the plant. The vascular tissue system consists of two complex tissues, the phloem and the xylem.

Figure 1.26 Leaf epidermis. (A) Replica of leaf epidermis from the cherry laurel (*Prunus laurocerasus*), showing stomata and irregularly shaped epidermal cells. (B) Epidermal peel from *Tradescantia* sp. Note the stomatal guard cells with chloroplasts.

Figure 1.27 Cell types found in the ground tissue system. (A) Parenchyma cells in the pith of a *Helianthus* stem. (B) Confocal image of collenchyma cells from a celery petiole (stalk); red asterisks indicate cell wall thickening at the corners of cells. (C) Sclereids (S) in *Trochodendron* leaf cells.
1.8.2 Vascular tissues are specialized for long-distance transport

The vascular tissue system is composed of two complex, long-distance transport tissues: xylem and phloem (see Table 1.2). Xylem tissue contains tracheary elements through which long-distance water transport occurs. It also contains xylem parenchyma cells and fibers. Phloem tissue contains sugar-conducting sieve tubes and their companion cells. Phloem parenchyma cells and fibers are also found in phloem.

1.8.3 Long-distance transport of water occurs in tracheary elements

Tracheary elements comprise two cell types, tracheids and vessel elements (Figure 1.28); they have thick, highly lignified, secondary cell walls and are dead and hollow at functional maturity. The pattern of secondary cell wall deposition in tracheary elements varies. Secondary cell walls of tracheary elements that differentiate in tissue that is still elongating are laid down in rings or in spiral bands. In regions of the plant where elongation has ceased, secondary walls of tracheary elements form a solid sheet with gaps called pits. Columns of vessel elements or tracheids stacked end to end form the pipes in which water and dissolved minerals are transported in xylem; these columns extend from the deepest roots to the tips of the tallest stems. Columns of vessel elements are called vessels. Tracheids are found in the xylem of all vascular plants, while vessels are found almost exclusively in angiosperms. Tracheids are long and narrow with tapered ends. They have pits in their end walls and side walls. Pits can be simple pores or more complex structures, e.g. the bordered pits found in tracheary elements of some gymnosperms (Figure 1.28). Vessel elements are shorter and wider than tracheids; they may be up to 700 μm in diameter. There are pits in the side walls of vessel elements; however their end walls have large perforations that allow water to flow unimpeded from cell to cell. In addition to water transport, tracheary elements provide structural support, allowing some vascular plants to reach heights of more than 100 m.

1.8.4 Long-distance transport of organic solutes occurs in sieve tubes

In all vascular plants except angiosperms, long-distance transport of sucrose and other organic molecules takes place in tubes formed by stacks of elongate sieve cells. These cells, in contrast to tracheary elements, have thin primary cell walls and are alive at functional maturity. In angiosperms, organic solute transport occurs through stacked sieve tube members also known as sieve elements. These cells lack a nucleus, vacuole and several other organelles, but they have a functional plasma membrane and therefore are alive (Figure 1.29). Cytoplasmic strands connect adjacent sieve tube members in a stack. The perforated end walls of these cells are called sieve plates. Adjacent to each sieve tube member and connected to it by numerous plasmodesmata (see Chapters 5 and 14) is a companion cell containing a nucleus and the other organelles usually found in living plant cells. Companion cells play a key role in the metabolism of sieve tube members and participate in loading sucrose into sieve tube members for long-distance transport (see Chapter 14).

Key points The evolution of vascular tissue that efficiently transport water and organic solutes was key to establishing plant life on land. Water is transported upward in the xylem. In angiosperms water-conducting cells in the xylem consist of tracheids and vessel elements, but in almost all gymnosperms xylem has only tracheids. Whereas tracheids are elongated cells connected to neighboring tracheids by pores called pits, vessels form a stacked series of dead cells that form unobstructed tubes for water movement through perforated end walls. Organic solutes are transported bidirectionally in the phloem. In angiosperms, phloem contains living sieve tube elements that lack a nucleus but have a nucleated companion cell associated with them. Sieve tube elements have highly perforated end walls called sieve plates and large cytoplasmic connections so that stacked elements form continuous tubes. Phloem transport, called translocation, requires living sieve cells.

1.9 The seed plant body plan II. Form and function of organ systems

We have seen that the cells of a plant are organized in tissues and tissue systems, each of which serves a different function. Now we will examine how these cells and tissues are arranged in roots, stems and leaves and how they contribute to the functions of each organ.
1.9.1 The root system acquires water and minerals

The root system is highly branched and generally has a larger surface area than the shoot system. The primary functions of roots are to absorb water and minerals from the soil, firmly anchor the plant and store carbohydrate. In most gymnosperms and eudicots, the radicle of the embryo becomes the primary root forming a taproot. The production of branched lateral roots further increases root surface area. Taproots can penetrate to
Figure 1.29 Phloem structure. (A) A longitudinal view of a sieve tube member and companion cell in the phloem. (B) Light micrograph of a longitudinal section of phloem from *Cucurbita pepo*. (C) A face view of a sieve plate; dark areas are cytoplasmic connections passing through holes in the sieve plate. (D) Light micrograph of a cross-section through phloem in *C. pepo* showing sieve tube elements, including a face view of a sieve plate, and companion cells.

great depths in the soil (Figure 1.30). Roots of mesquite, a desert shrub, can reach depths of 100 m. Taproots of carrots and beets are modified for increased food storage. In monocots, such as cereals and other grasses, the seedling primary root usually dies and is replaced by adventitious roots, produced from the base of the stem. These roots form a fibrous root system that spreads laterally in the soil and efficiently absorbs water and minerals from surface layers of soil. The ecological differences between these two root systems can be seen in an unwatered lawn during warm summer months. Grasses, with fibrous root systems, often turn brown while the leaves of eudicot weeds such as dandelion, that have deep taproots, remain green.
Figure 1.30 Two types of root systems. (A) A taproot system extends deeply into the soil. (B) A fibrous root system extends laterally near the soil surface rather than to great depths. The vertical distance between lines represents about 30.5 cm.

1.9.2 Primary tissues of the root consist of the central stele surrounded by the cortex and epidermis

The primary anatomy of a mature root of a eudicot is shown in Figure 1.31. At the center of the root is a core of vascular tissue, called the vascular cylinder or stele. In the roots of cone-bearing gymnosperms and most eudicots, primary xylem occupies the center of the stele; transverse sections through the stele show that the xylem resembles a star with three, four or five points. Primary phloem is found in notches between the points of the star. In monocot roots, on the other hand, a core of ground tissue called pith is located at the center of the stele. Concentric rings of primary xylem (next to the pith) and primary phloem surround the pith. In all cases, a layer of unspecialized cells, the pericycle, forms the outer boundary of the vascular cylinder. Between the epidermis and vascular cylinder is ground tissue called cortex. Cells of the cortex store reserves, mostly starch.

The innermost layer of cortex cells is the endodermis. Periclinal walls (arranged at right angles to the root surface) of endodermal cells are impregnated with a waxy polymer, suberin; this layer is called the Casparian strip (Figure 1.31C). The plasma membrane of endodermal cells is firmly attached to the Casparian strip, creating a barrier that prevents diffusion of water and solutes along endodermal cell walls. Solute must cross the plasma membranes of endodermal cells before they can reach the vascular system (see Chapter 13).
1.9.3 The shoot system is organized into repeating modules

The shoot system consists of two organs, leaves and stems; it also produces reproductive organs (see Figure 1.23). The shoot system is organized into repeating modules called phytomers. Each phytomer consists of a node, where leaves and axillary buds attach to the stem, and an internode, the stem between nodes. Leaves display a variety of forms; they are major photosynthetic organs converting water, carbon dioxide and light energy to carbohydrate (Figure 1.32). Stems connect underground roots with aerial leaves, conducting water and minerals from the roots to the leaves, and photosynthate from the leaves to the roots. Some stems, such as potato (Solanum tuberosum) tubers, iris (Iris spp.) rhizomes and crocus (Crocus spp.) corms, are modified for food storage, while others, such as cactus stems, are modified for water storage (Figure 1.33).

1.9.4 The tissues of an angiosperm leaf consist of an epidermis with stomata, photosynthetic mesophyll cells and veins

The arrangement of tissues in a generalized leaf is shown in Figure 1.34. An epidermis with cuticle surrounds the inner tissues of leaves. Stomata occur in the epidermis and their location and density varies from species to species (see Chapter 14). The ground tissue in angiosperm leaves is made up mostly of parenchyma cells that are specialized for photosynthesis and contain many chloroplasts. Photosynthetic parenchyma cells in leaves are often called mesophyll (meso = middle, phyll = leaf). In many angiosperms, there are two distinct types of parenchyma: tightly packed, elongate palisade parenchyma, located toward the adaxial surface, and loosely packed spongy parenchyma, found

Figure 1.32 Variations in leaf morphology. Simple leaves (C–H) have an entire blade, while in compound leaves (A, B, I) the blade is divided into leaflets. Blades of leaves range in size and shape; some are broad (e.g. C and E) whereas others are narrow (H) or even needle-like (J). There is also variation in petiole length; some are long (e.g. C, E, and K) while others are short (e.g. G) and some leaves lack petioles (D and F).
abaxially. The air spaces between spongy parenchyma cells favor rapid gas exchange to palisade cells. Collenchyma and sclerenchyma may also be found in leaf ground tissue, usually associated with major veins.

Vascular tissue in leaves is found in veins embedded in the ground tissue. The interconnected system of veins in a leaf is highly branched so that no cell in a leaf is far from a vein. In each vein, xylem occupies the adaxial half of the vein and phloem is found in the abaxial half. Veins are often surrounded by a bundle sheath of parenchyma cells. In most angiosperms, bundle sheath cells do not have chloroplasts but bundle sheath cells of plants with C₄ photosynthesis, such as Zea mays (maize), are packed with chloroplasts (see Chapter 9). In the leaves of most eudicots and primitive dicots, veins occur in a reticulate (netted) pattern with a main vein that forms the midrib of a leaf and branches into progressively smaller veins. In most monocot leaves, veins run parallel to each other along the length of a leaf.

1.9.5 Primary tissues of the stem are organized differently in monocots and eudicots

The organization of tissues in typical monocot and eudicot stems is shown in Figure 1.35. The outmost layer
of cells is the epidermis with a waxy cuticle. In green stems the epidermis may contain stomata as well as hairs and glands. In transverse section, vascular tissue of stems occurs in **vascular bundles**. Each bundle is divided into **xylem** and **phloem**. Usually xylem is located on the inner half of a bundle and phloem in the outer half. In the stems of most eudicots and gymnosperms that have only undergone primary growth, a ring of vascular bundles divides the ground tissue into two regions, an outer **cortex** between the epidermis and vascular bundles, and an inner **pith**, ringed by vascular bundles. This differs from the arrangement of vascular bundles in monocots, such as maize, in which vascular bundles are scattered through the ground tissue. In green stems, the cells in the outer layers of cortex contain chloroplasts and are photosynthetic.

**Figure 1.34** Organization of tissue systems in a eudicot leaf. (A) Light micrograph of a transverse section of the main vein of a leaf showing vascular tissue (main vein), ground tissue, and upper and lower epidermis. In this leaf stomata are found in the lower (abaxial) epidermis. (B) Light micrograph of a transverse section of a leaf blade. In this leaf, the ground tissue is divided into palisade and spongy parenchyma. A small vein containing xylem and phloem can be seen.

**1.10 The seed plant body plan III. Growth and development of new organs**

Now that we have considered the organization of the plant body, we can examine how this body grows and develops. In contrast to animals, a plant continues to grow and produce organs repeatedly throughout its life. New organs are initiated in localized centers of cell division called **meristems**. Primary growth occurs at the tips of roots and stems and leads to increase in length. Secondary growth may occur in mature tissues of roots and stems; this results in an increase in diameter.
1.10.1 Apical meristems produce the primary plant body

Meristems are localized groups of dividing cells. Apical meristems, found at the tips of roots and growing points of shoots, are made up of unspecialized, dividing meristematic cells. Cells produced by these meristems allow continuous growth of the root and stem. In addition, the shoot apical meristem produces cells that will become new organs: leaves and axillary buds, potential branches. Thus plants have indeterminate growth, increasing in size and producing new organs throughout their lives. Cells derived from apical meristems form the three primary meristems of roots and shoots: the protoderm, the ground meristem and the procambium. As we have seen, each of these primary meristems produces one of the three tissue systems that make up a plant, respectively the dermal, ground and vascular tissue systems. Tissues that derive from primary meristems are called primary tissues and the increase in length that results from their action is called primary growth.

Key points Plants differ from animals in possessing groups of cells that in principle can grow and divide indefinitely. Meristems are defined as zones of undifferentiated cells that can undergo mitosis to produce new cells that differentiate into mature tissues. Apical meristems at the tips of stems and roots are responsible for primary growth, and long-lived species such as bristlecone pines (Pinus longaeva) owe their longevity in part to apical meristems. In woody plants lateral meristems are responsible for producing secondary tissues: secondary phloem and secondary xylem as well as cork in secondary growth. Lateral meristems are found in both stems and roots, in fact woody shoots and roots are almost impossible to distinguish from each other after several years of secondary growth.
1.10.2 The root apex consists of the meristem covered by the root cap, and lateral roots originate as primordia in the pericycle

There are many important differences in primary growth and the production of new organs in roots and shoots. We will look at these processes first in roots and then in shoots. The organization of the root apex is shown in Figure 1.36. In roots, the apical meristem is covered by a root cap that protects the root as it pushes through soil. As the root grows, root cap cells are sloughed off and are continually replaced by the apical meristem. The outermost cells of the root cap produce a polysaccharide slime that lubricates the tip as it moves through the soil. Roots may produce a prodigious amount of slime; it has been estimated that a large plant, with thousands of roots, can invest as much as 10% of all carbon produced in photosynthesis in slime production.

In most roots cell elongation is confined to the apical 10 mm behind the apical meristem. In the zone of cell elongation cells may increase in length 20–50 times. Some cell differentiation occurs in this zone, however most differentiation, including the production of root hairs, takes place in the zone of cell maturation after elongation has ceased (Figure 1.36).

The initiation of branch (= lateral) roots occurs in mature parts of a root (Figure 1.37). Cells of the pericycle are triggered to divide to form a group of cells, a branch root primordium. The primordium develops into a new root, with its own apical meristem; it burrows through the cortex and epidermis of the parent root until it reaches the outside. As vascular tissues in the basal end of the lateral root mature, they connect to the vascular cylinder of the main root.

1.10.3 The shoot apical bud is the source of leaves, axillary buds and floral organs

The organization of the shoot apex, the shoot apical bud, differs from that of the root tip (Figure 1.38). In addition to adding cells to primary meristems, the shoot apical meristem produces cells that will become new leaves and axillary buds or, under certain conditions, floral organs. Leaf primordia arise as groups of cells on the sides of the apical meristem. As cell division continues young leaves increase in size and arch over the apical meristem. In the axil of each leaf, cells derived from the apical meristem divide to form axillary buds, miniature, dormant (non-growing) replicas of the shoot apical bud. Cell elongation in the stem is somewhat delayed so the apical bud of a stem contains a number of nodes with very short internodes. When axillary buds start to grow they become lateral branches. If axillary buds grow soon after they are formed, a plant will have a ‘bushy’ appearance as in the ornamental plant Coleus. If axillary buds remain dormant, the plant will have a monopodial growth habit and lack branches (e.g. in tobacco, sunflower, etc.) (Figure 1.39).

1.10.4 Secondary growth is for the long haul, up to thousands of years

Many plants, such as monocots and herbaceous eudicots, increase in size only by primary growth, all cells being added by primary meristems. In gymnosperms and woody angiosperms, stems and roots increase in diameter as well as in height by secondary growth. During secondary growth, most of the tissues of the plant body are produced not by apical meristems, but by lateral meristems. Lateral meristems give rise to secondary tissues, and the consequent increase in plant size is termed secondary growth. Secondary growth is often associated with extreme size and longevity, as in trees such as the bristlecone pine and giant sequoia (see Section 1.6.2).

1.10.5 Lateral meristems allow for expansion in girth

In some species, secondary growth may increase the diameter of the stem from 1–2 cm to 10–15 m, and woody trees can reach heights in excess of 100 m. Growth in girth, sometimes referred to as secondary thickening, is initiated in parts of the root and stem that are no longer increasing in length. Two lateral meristems are involved in secondary growth: the vascular cambium, which produces secondary xylem and secondary phloem, and cork cambium, which produces periderm, a waterproof, protective outer coating of cells. Although most monocots lack secondary meristems, many, notably various species of palm, can increase in circumference
Figure 1.36  Primary growth in the root. (A) Elongating primary roots have an apical meristem that produces cells in two directions: acropetally to replenish the protective root cap; and basipetally to add cells to the elongation zone, where cells increase in length 20–50-fold. Cell differentiation primarily occurs after cell elongation has ceased. (B) At the edge of the vascular cylinder, in mature tissue, division of the pericycle produces lateral root primordia. (C) Developing lateral roots burrow through the root cortex, and eventually burst through the epidermis and grow into the soil.
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Figure 1.37 Light micrographs showing lateral root formation. (A) Longitudinal section of a *Lupinus* root showing two stages of lateral root formation. (B) Transverse section of lateral root formation in willow (*Salix*). Lateral roots arise by division of pericycle cells. The root primordium burrows through the cortex and epidermis of the parent root to reach the soil.

because structures such as leaf bases become lignified, die and persist, providing support for the stem.

Within the stem, a continuous ring of **vascular cambium** arises from undifferentiated remnants of procambium that are located between the phloem and xylem of vascular bundles and from **interfascicular cambium** produced by the dedifferentiation of parenchyma cells located between the vascular bundles (Figure 1.40). In the root, vascular cambium forms in the stele from residual procambium that surrounds the primary xylem. In both stems and roots, cells in the ring of vascular cambium divide periclinally, producing tiers of cells in both radial directions. Secondary xylem is produced toward the center of a stem or root, while secondary phloem is produced toward the organ surface. At intervals, the vascular cambium produces files of parenchyma cells called **rays** both centripetally (toward the center of the organ) and centrifugally (toward the outside). Ray cells store starch and permit radial transport of water, inorganic ions and organic solutes across the woody stem and root. Cells of the vascular cambium also divide anticlinally (perpendicular to the surface of the organ) increasing the diameter of the cambium.

As growth proceeds from year to year, layers of secondary xylem accumulate forming **wood**. In an older tree trunk, one can see a distinction between darkly colored **heartwood**, at the center of the trunk, and paler, younger **sapwood** (Figure 1.41). In this case, water transport only occurs in sapwood. The tracheary elements of heartwood are filled with various polymers thought to be waste products that are deposited in the xylem for permanent storage.

Tissues outside the vascular cambium, including the primary and secondary phloem, the cortex and the epidermis cannot accommodate the increase in circumference. Periodically, outer layers split and are
sloughed off. To replace the protective epidermis, another lateral meristem, the cork cambium, initially arises in the outer layers of the cortex in the stem and from the pericycle cells of the root. The division of cells in the cork cambium produces cork (phellem) to the outside and parenchyma called phelloderm toward the inside. Cork cells are dead at functional maturity. Their cell walls contain lignin and suberin, which act to waterproof the outer parts of the organ (Figure 1.42). Slit-like openings in the cork, called lenticels, form at sites where the cork cambium generates a spongy tissue that, unlike cork, has many air spaces between the cells. The lenticels allow for gas exchange between the atmosphere and the living cells in the woody stem.

The bark of a tree consists of all the tissue outside the vascular cambium; the inner bark is made up of functional secondary phloem, and the outer bark contains alternating layers of cork and non-functional, older secondary phloem. A tree accumulates all the xylem tissue it produces, but only a few years worth of functional secondary phloem are present. Removing a ring of bark around the circumference of a tree, a practice called ‘ringing’ or ‘girdling’, removes phloem thus interrupting the flow of photosynthate to the roots and the tree will die.

**Figure 1.39** Apical dominance affects the overall morphology of a plant. (A) Some plants, such as Coleus, have weak apical dominance resulting in a low, highly branched morphology. (B) In species such Hibiscus, apical dominance is much stronger, producing a plant with a single main stem with few to no branches.

1.10.6 Wood morphology is influenced by environmental and endogenous factors

The activity of the vascular cambium can be regulated by day length. In trees that grow in temperate latitudes where there are seasonal changes in day length, the cambium ceases to divide with the onset of the short days of fall. The last cells produced by the cambium in the fall have small diameters and thick walls. Tracheary elements, produced when cambial division is reinitiated in spring, are larger and have thinner walls than those produced in late summer. Annual growth rings in the xylem are delineated by the contrast between the late summer wood of one year and spring wood of the next year (Figure 1.43). The amount of xylem produced in a given year is influenced by a number of factors including temperature, water availability and nutrient availability. The measurement of changes in annual rings has given rise to the science of dendrochronology in which the pattern of annual rings can be linked to specific dates. In this way dendrochronologists can accurately determine the age of a tree and can date when a specific piece of wood was formed. Annual rings can be used to estimate
Figure 1.40 Secondary growth in the shoot. The activity of two lateral meristems—the vascular cambium and the cork cambium—increase stem circumference in many gymnosperms and non-monocot angiosperms. The vascular cambium produces secondary phloem outward and secondary xylem (wood) inward. The cork cambium produces layers of cork that form a portion of the outer bark.
the age of a tree and the climatic history of the area in which the tree is growing (see Section 17.2.3). Trees that grow in tropical latitudes, characterized by little or no seasonal change in day length, often do not show growth rings. However, in areas with wet and dry seasons, similar growth rings are produced when cambial growth stops in the dry season and restarts in the wet season.

**Key points** Many common and technical names have been used to describe tissue in mature trees and these include bark and cork for the outer layers, and sapwood and heartwood, and soft wood and hard wood for secondary xylem. Bark is a non-technical term for all tissue in a stem or root that lies outside the vascular cambium and includes the secondary phloem and cork. Removing the bark from a tree is often referred to as ring girdling. It will kill the tree because all transport in the phloem is interrupted. Sapwood and heartwood refer to two zones in secondary xylem that can be distinguished by their appearance. Heartwood is located at the center of the stem and is darker in color as a result of the deposit of a range of natural, antimicrobial products. The outer layers of wood are called sapwood and are lighter in color because deposits in these cells are absent; this tissue is where water transport occurs. Heartwood is generally more resistant to decay by fungi and other microorganisms and is therefore more highly sought after in construction. Soft wood and hard wood are terms that refer to the physical properties of wood that result from the presence or absence of vessels and fibers. Soft wood is most generally found in gymnosperms; it lacks vessels and is a tissue of uniform consistency and is relatively easy to work, i.e. chisel, plane or saw. Hard wood is found in angiosperms and consists of a mixture of tracheids and vessels, making it harder to work.
Figure 1.43 Annual rings in secondary xylem of a gymnosperm (*Pinus*) (left) and an angiosperm (*Tilia*) (right). Growth rings are formed because of differences in sizes of cells produced in spring (early wood, large cells) and summer/fall (late wood, very small cells). The very small cells of late wood form a distinct demarcation with the cells of the following spring. The easiest way to count annual rings is to count the number of lines that late wood makes in the secondary xylem.