

The reproductive structures of an ornamental poppy (*Papaver rhoeas*). Male gametophytes, which produce pollen, surround the female gametophyte, which produces eggs and is the site of fertilization and seed development (photographer's close-up).

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## STUDY PLAN

### 34.1 Overview of Flowering Plant Reproduction

Diploid and haploid generations arise in the angiosperm life cycle

### 34.2 The Formation of Flowers and Gametes

In angiosperms, flowers contain the organs for sexual reproduction

Pollen grains arise from microspores in anthers

Eggs and other cells of female gametophytes arise from megaspores

### 34.3 Pollination, Fertilization, and Germination

Pollination requires compatible pollen and female tissues

Double fertilization occurs in flowering plants

The embryonic sporophyte develops inside a seed

Fruits protect seeds and aid seed dispersal

Seed germination continues the life cycle

### 34.4 Asexual Reproduction of Flowering Plants

Vegetative reproduction is common in nature

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### 34.5 Early Development of Plant Form and Function

Within hours, an early plant embryo's basic body plan is established

Key developmental cues are based on a cell's position

Morphogenesis shapes the plant body

Regulatory genes guide the development of floral organs

Leaves arise from leaf primordia in a closely regulated sequence

# 34 Reproduction and Development in Flowering Plants

## WHY IT MATTERS

Seeds of a small flowering tree, *Theobroma cacao*, produce the raw material that modern confectioners turn into chocolate. The tree evolved in the undergrowth of tropical rain forests in Central America, where it was domesticated by the Maya and Aztec peoples. Today cacao trees flourish on vast plantations in the tropical lowlands of Central and South America, the West Indies, West Africa, and New Guinea. Unlike most angiosperms, which produce flowers at the tips of floral shoots, *T. cacao* flowers grow directly from buds on the tree trunk. The flowers are pollinated by insects, primarily midges of the genus *Forcipomyia*. Pollination is the first step toward fertilization of the eggs, and within about 6 months, large, heavy fruits develop from them (Figure 34.1). Each podlike fruit contains from 20 to 60 seeds—the cacao “beans” that chocolate manufacturers process into cocoa, chocolate, and other commercial products.

As in other flowering plants, cacao seeds result from sexual reproduction. Angiosperms have elaborate reproductive systems—housed in flowers—that produce, protect, and nourish sperm, eggs, and developing embryos. As with cacao, the flowers of many species also serve as invitations to animal pollinators, which function in



**Figure 34.1**  
Flowers and fruits growing from the trunk of a cacao tree (*Theobroma cacao*), in Central America. Each fruit is the mature ovary of a *T. cacao* flower.

bringing sperm and egg together. Once a new individual forms and begins to grow, finely regulated gene interactions guide the development of flowers and other plant parts. Under certain circumstances, many plants—including cacao—also reproduce asexually, so that individuals of the new generation are clones, genetically identical to their parents.

Sexual reproduction dominates the life cycle of flowering plants, however, and it will be our main focus in the first three sections of this chapter. We then consider asexual reproduction and conclude with a discussion of early plant development. Using methods of molecular biology and a variety of model organisms, plant biologists are beginning to elucidate some of the mechanisms by which plant developmental pathways unfold.

### 34.1 Overview of Flowering Plant Reproduction

In the living world, sexual reproduction occurs when male and female haploid gametes unite to create a fertilized egg. This fertilized egg—the diploid zygote—then embarks on a developmental course of mitotic cell divisions, cell enlargement, and cell differentiation. In flowering plants, subsequent steps result in distinctive haploid and diploid forms of the individual.

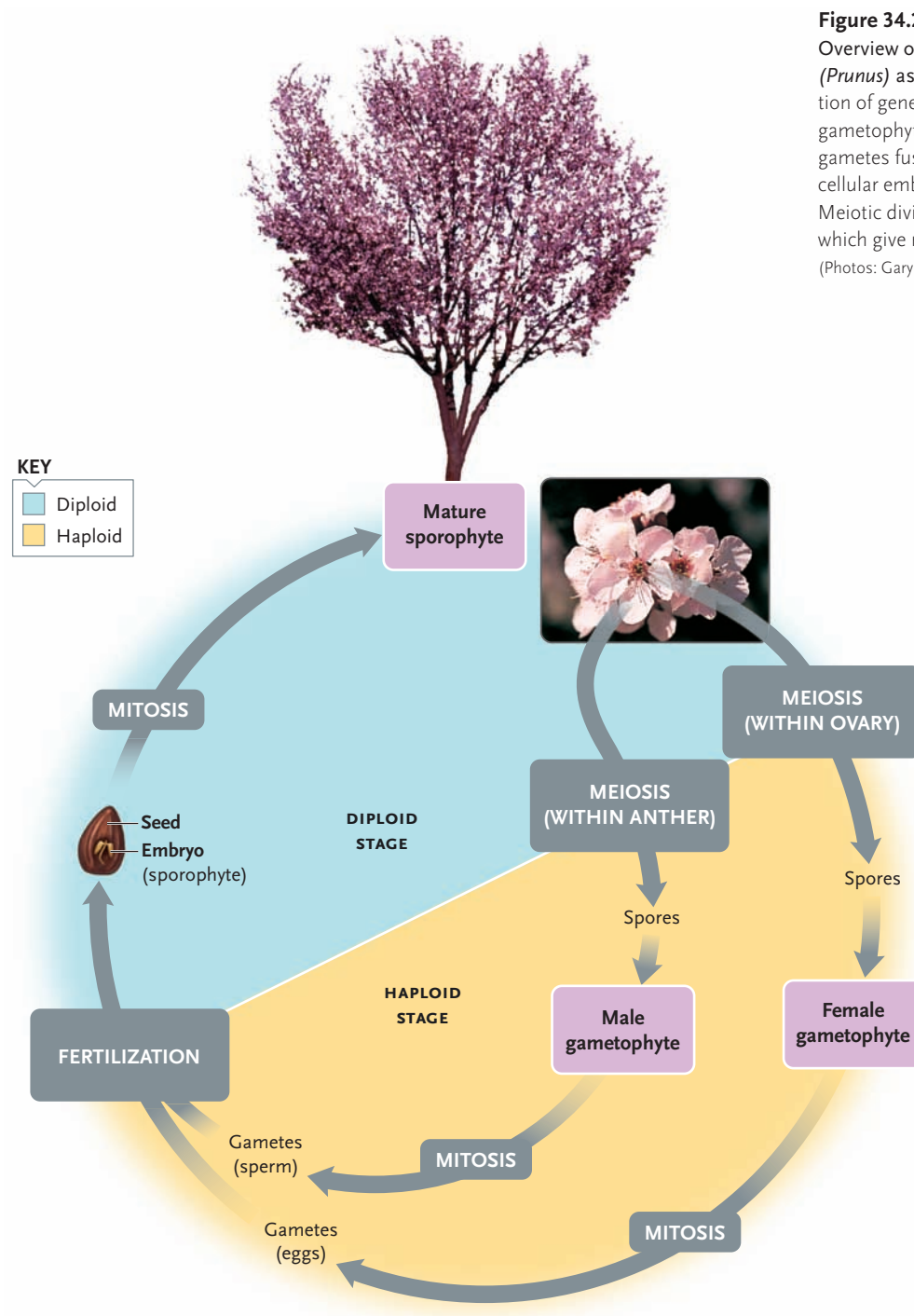
#### Diploid and Haploid Generations Arise in the Angiosperm Life Cycle

Once an angiosperm zygote has formed, the developmental sequence generates an embryo enclosed within a seed. In a seed, early versions of the basic plant tissue systems are already in place, so the embryo technically is already a **sporophyte**—the diploid, spore-producing body of a plant (see Section 27.1).

When most people look at a cherry tree or a rosebush, what they think of as “the plant” is the sporophyte (**Figure 34.2**).

At some point during one or more seasons of an angiosperm sporophyte’s growth and development, one or more of its vegetative shoots undergo changes in structure and function and become *floral shoots*—that is, reproductive shoots that will give rise to a flower or inflorescence (a group of flowers on the same floral shoot). Certain cells in the flowers divide by meiosis. Unlike in animals, however, meiosis in plants does not yield gametes directly. Instead, meiosis gives rise to haploid **spores**, walled cells that develop by mitosis into multicellular haploid **gametophytes**. The gametophytes produce haploid sex cells, the gametes, again by mitosis. Male gametophytes produce sperm cells, the male gametes of flowering plants; female gametophytes produce eggs. This division of a life cycle into a diploid, spore-producing generation and a haploid, gamete-producing one is called **alternation of generations** (a phenomenon described more fully in Chapter 27).

In virtually all plants, the gametophyte and sporophyte are strikingly different from one another in both function and structure. For instance, in bryophytes (mosses and liverworts) the gametophyte is usually larger than the sporophyte; the sporophyte grows out of the gametophyte and is nourished by it (see Section 27.2). In ferns, which are seedless vascular plants, the gametophyte is much smaller than the sporophyte and is free-living for much of its lifespan; in most fern species the gametophyte nourishes itself by photosynthesis. In angiosperms and other seed plants, gametophytes are small structures that are retained *inside* the sporophyte for all or part of their lives. The female gametophyte of a flowering plant usually consists of only seven cells that are embedded in floral tissues, as you will read shortly. Male gametophytes are released into the environment as pollen grains, so small that they



**Figure 34.2**

Overview of the flowering plant life cycle, using the cherry (*Prunus*) as an example. This type of reproductive cycle, alternation of generations, has a haploid phase in which multicellular gametophytes produce gametes and a diploid phase in which two gametes fuse to form a zygote. This zygote develops into a multicellular embryo within a seed and then into a mature sporophyte. Meiotic divisions in the flower of the sporophyte produce spores, which give rise to new gametophytes.

(Photos: Gary Head.)

are measured in micrometers. The pollen grain matures when it reaches a compatible ovule, resulting in fertilization and production of a new generation of seeds.

Sporophytes may also reproduce asexually. For instance, strawberry plants send out horizontal stolons, and new roots and shoots develop at each node along the stems. Short underground stems of onions and lilies put out buds that grow into new plants. In summer and fall, Bermuda grass produces new plants at nodes along its subterranean rhizomes. Asexual reproduction also can be induced artificially. Whole orchards of genetically identical fruit trees

have been grown from cuttings or buds of a single parent tree.

We turn now to our consideration of sexual reproduction in angiosperms, beginning with the crucial step in which flowers develop.

### STUDY BREAK

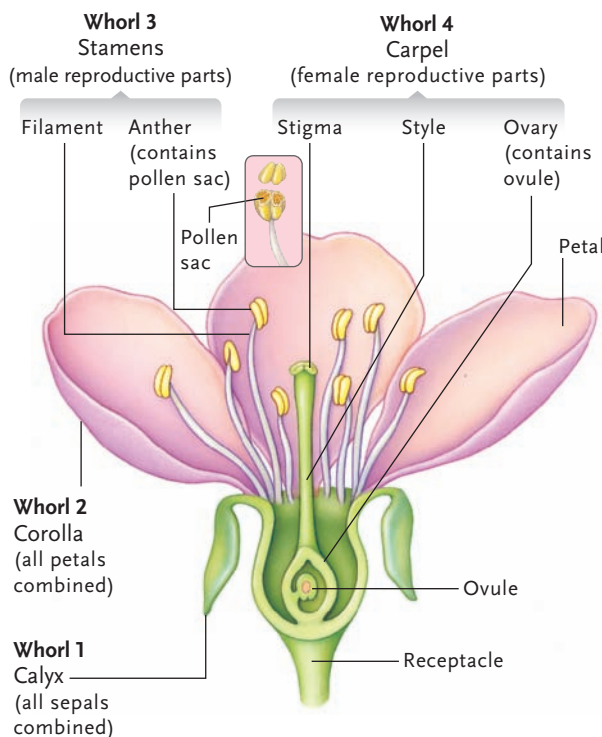
1. What are the two “alternating generations” of plants?
2. How do these two life phases differ in structure and function?

## 34.2 The Formation of Flowers and Gametes

Flowering marks a developmental shift for an angiosperm. Biochemical signals—triggered in part by environmental cues such as day length and temperature—travel to the apical meristem of a shoot and set in motion changes in the activity of cells there. Instead of continuing vegetative growth, the shoot is modified into a floral shoot that will give rise to floral organs.

### In Angiosperms, Flowers Contain the Organs for Sexual Reproduction

A flower develops from the end of the floral shoot, called the **receptacle**. Cells in the receptacle differentiate to produce up to four types of concentric tissue regions called *whorls*. The arrangement and number of whorl types varies in different species; **Figure 34.3** shows a typical example in which a flower has one of each of the four whorls. The two outer whorls consist of nonfertile, vegetative structures. The outermost whorl (whorl 1), the **calyx**, is made up of leaflike **sepals**. The calyx is usually green, and, early in the flower's development, it encloses all the other parts, as in an unopened rose bud. The next whorl, the **corolla**, includes the **petals**. Corollas are the “showy” parts of



**Figure 34.3**

Structure of a cherry (*Prunus*) flower, with the four whorls indicated. Like the flowers of many angiosperms, it has a single carpel and several stamens. The anthers of the stamen produce haploid pollen. The stigma of the carpel receives the pollen, and the ovule inside the ovary contains the haploid eggs.

flowers; they have distinctive colors, patterning, and shapes, and these features often function in attracting bees and other animal pollinators.

A flower's two inner whorls are specialized for making gametes. Inside the corolla is the whorl of **stamens** (whorl 3), in which male gametophytes form. In almost all living flowering plant species, a stamen consists of a slender **filament** (stalk) capped by a bilobed **anther**. Each anther contains four **pollen sacs**, in which pollen develops.

The innermost whorl (whorl 4) consists of one or more **carpels**, in which female gametophytes form. The lower part of a carpel is the **ovary**. Inside it is one or more **ovules**, in which an egg develops and fertilization takes place. A seed is a mature ovule. In many flowers that have more than one carpel, the carpels fuse into a single, common ovary containing multiple ovules. Typically, the carpel's slender **style** widens at its upper end, terminating in the **stigma**, which serves as a landing platform for pollen. Fused carpels may share a single stigma and style, or each may retain separate ones. The name angiosperm (“seed vessel”) refers to the carpel.

Some species have so-called **complete flowers**, in which all four whorls are present. In other species, flowers lack one or more of the whorls, and thus botanists describe them as **incomplete flowers** (**Figure 34.4**). Botanists also distinguish flowers on the basis of the sexual parts they contain. Most angiosperms produce **perfect flowers**, which have both kinds of sexual parts—that is, both stamens and carpels. **Imperfect flowers** are a type of incomplete flower that has stamens or carpels, but not both. (Notice that all imperfect flowers are also incomplete.) Species with imperfect flowers are further divided according to whether individual plants produce both sexual types of flowers, or only one. In **monoecious** (“one house”) species, such as oaks, each plant has some “male” flowers with only stamens and some “female” flowers with only carpels. In **dioecious** (“two houses”) species, such as willows, a given plant produces flowers having only stamens or only carpels. With this basic angiosperm reproductive anatomy in mind, we now turn to the processes by which male and female gametes come into being.

### Pollen Grains Arise from Microspores in Anthers

Most of a flowering plant's reproductive life cycle, from production of sperm and eggs to production of a mature seed, takes place within its flowers. **Figure 34.5** shows this cycle as it unfolds in a perfect flower. The spores that give rise to male gametophytes are produced in a flower bud's anthers (see **Figure 34.5**, left). The pollen sacs inside each anther hold diploid microsporocytes (or *microspore mother cells*); each microsporocyte undergoes meiosis and eventually produces four small haploid **microspores**. Like most plant cells, the

a. Complete flower of an apple tree (*Malus*)



b. Incomplete flower of a Hubbard squash (*Cucurbita*)



**Figure 34.4**

Examples of complete and incomplete flowers.

(a) Apple flowers (*Malus*) are complete. Each has many stamens, carpels, and petals, along with petal-like sepals. (b) As with other plants in the pumpkin family, the flowers of this Hubbard squash (*Cucurbita maxima*) are both incomplete and imperfect because each has either stamens or carpels, but never both.

microspores are walled, and inside its wall each microspore divides again, this time by mitosis. The result is an immature, haploid male gametophyte—a **pollen grain**.

Of the two nuclei produced by the mitotic division of a microspore, one again divides. After this second round of mitosis the male gametophyte consists of three cells—two sperm cells plus a third cell that controls the development of a **pollen tube**. When pollen lands on a stigma, this tube grows through the tissues of a carpel and carries the sperm cells to the ovary. A mature male gametophyte consists of the pollen tube and sperm cells—the male gametes.

The walls of pollen grains are hardened by the decay-resistant polymer *sporopollenin*, and are tough enough to protect the male gametophyte during the somewhat precarious journey from anther to stigma. These walls are so distinctive that the family to which a plant belongs usually can be identified from pollen alone—based on the size and wall sculpturing of the grains, as well as the number of pores in the wall (**Figure 34.6**). Because they withstand decay, pollen grains fossilize well and can provide revealing clues about the evolution of seed plants and the ecological communities that lived in the past.

### Eggs and Other Cells of Female Gametophytes Arise from Megaspores

Meanwhile, in the ovary of a flower, one or more dome-shaped masses form on the inner wall. Each mass becomes an ovule (see Figure 34.5, right), which, if all goes well, develops into a seed. Only one ovule forms in the carpel of some flowers, such as the cherry. Dozens, hundreds, or thousands may form in the carpels of other flowers, such as those of a bell pepper plant (*Capsicum annuum*). At one end, the ovule has a small opening, called the **micropyle**.

Inside the cell mass, a diploid megasporocyte (or *megaspore mother cell*) divides by meiosis, forming four haploid **megaspores**. In most plants, three of these megaspores disintegrate. The remaining megaspore enlarges and develops into the female gametophyte in a sequence of steps tracked in Figure 34.5.

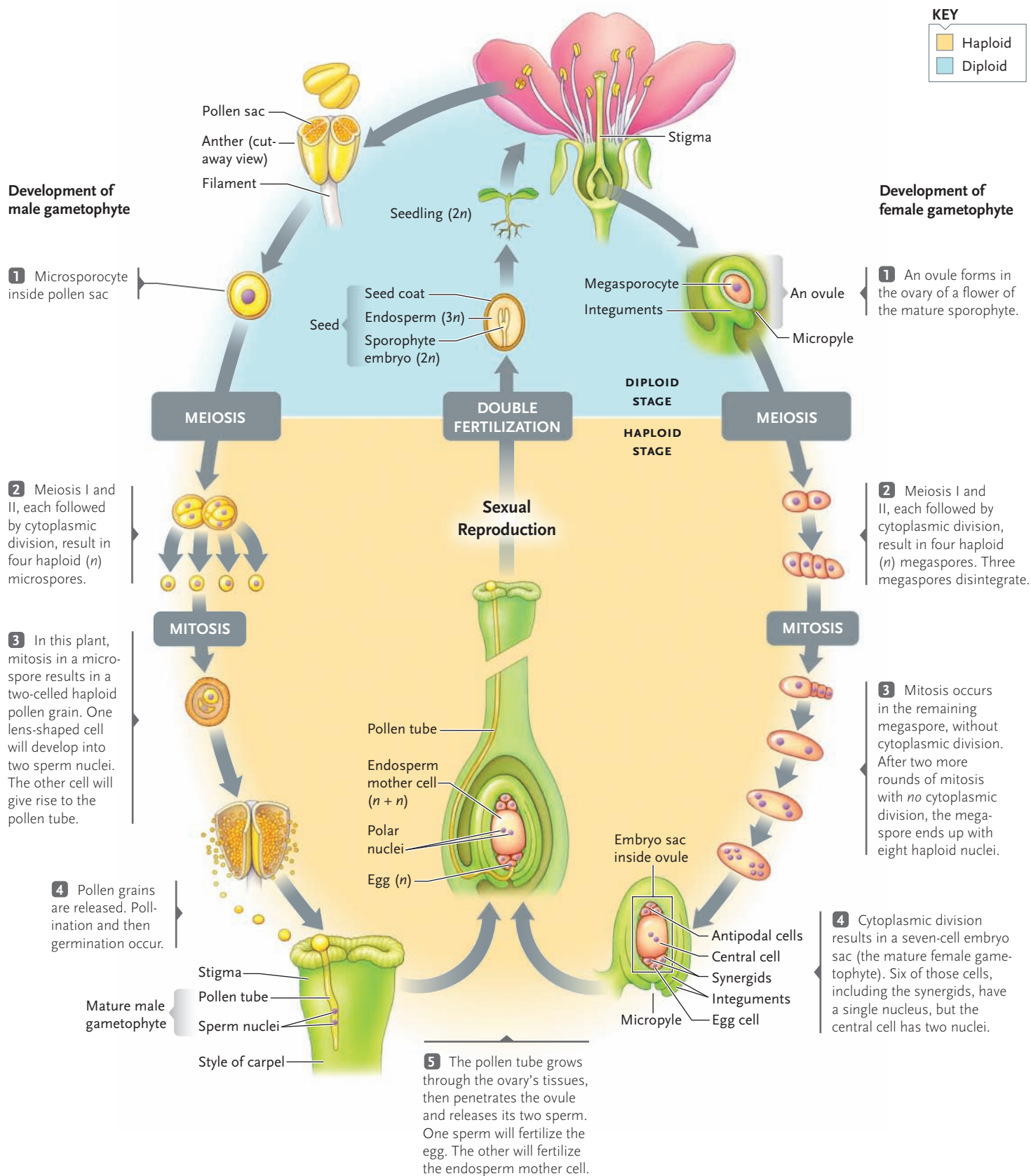
First, three rounds of mitosis occur *without* cytoplasmic division; the result is a single cell with eight nuclei arranged in two groups of four. Next, one nucleus in each group migrates to the center of the cell; these two **polar nuclei** (“polar” because they migrate from opposite ends of the cell) may fuse or remain separate. The cytoplasm then divides, and a cell wall forms around the two polar nuclei, forming a single large *central cell*. A wall also forms around each of the other nuclei. Three of these walled nuclei become *antipodal cells*, which eventually disintegrate. Three others form a cluster (called the “egg apparatus”) near the micropyle; one of them is an **egg cell** that may eventually be fertilized. The other two, called *synergids*, will have a role in pollination. The eventual result of all these events is an **embryo sac** containing seven cells and eight nuclei. This embryo sac is the female gametophyte.

In about a third of flowering plants, biologists have observed variations in the events that produce a female gametophyte. In lilies, for example, changes in the sequence of cell divisions produce several cells with triploid nuclei (see Figure 27.31). The egg cell is not involved, however, so such differences do not affect reproduction. They may have roles in the development and functioning of other embryonic tissues.

As the male and female gametophytes complete their maturation, the stage is set for fertilization and the development of a new individual.

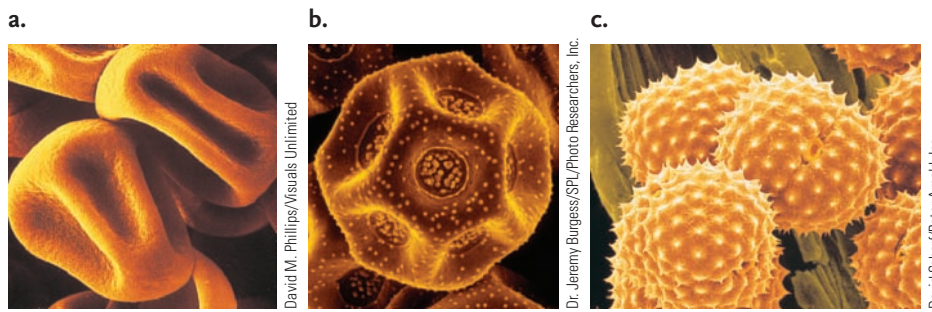
### STUDY BREAK

1. What is the biological role of flowers, and what fundamental physiological change must occur before an angiosperm can produce a flower?
2. Explain the steps leading to the formation of a mature male gametophyte, beginning with microsporocytes in a flower’s anthers. Which structures are diploid and which haploid?
3. Trace the development of a female gametophyte, beginning with the megasporocyte in an ovule of a flower’s ovary. Which structures are diploid and which haploid?



**Figure 34.5**

Life cycle of cherry (*Prunus*), a eudicot. Pollen grains develop in pollen sacs within the anthers. An embryo sac forms in the single ovule within the cherry flower's ovary, and an egg forms within the embryo sac. When the pollen grains are released and contact the stigma, double fertilization occurs. An embryo sporophyte and nutritive endosperm develop and become encased in a seed coat.



**Figure 34.6**  
Some examples of pollen grain diversity. Scanning electron micrographs of pollen grains from (a) a grass, (b) chickweed (*Stellaria*), and (c) ragweed (*Ambrosia*) plants.

### 34.3 Pollination, Fertilization, and Germination

The process by which plants produce seeds—which have the potential to give rise to new individuals—begins with *pollination*, when pollen grains make contact with the stigma of a flower. Air or water currents, birds, bats, insects, or other agents make the transfer. (Section 27.5 discussed the complex relationship between some flowering plants and their animal pollinators.)

Pollination is the first in a series of events leading to *fertilization*, the fusion of an egg and sperm inside the flower's ovary. The resulting embryo and its ovule mature into a seed housing a young sporophyte, and when the seed *germinates*, or sprouts, the sporophyte begins to grow.

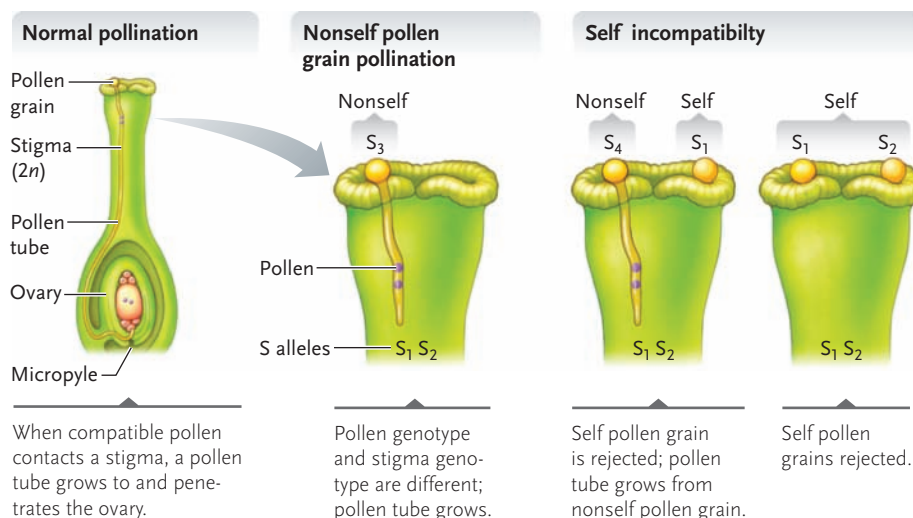
#### Pollination Requires Compatible Pollen and Female Tissues

Even after pollen reaches a stigma, in most cases pollination and fertilization can take place only if the pollen and stigma are compatible. For example, if pollen from one species lands on a stigma from another, chemical incompatibilities usually prevent pollen tubes from developing.

Even when the sperm-bearing pollen and a stigma are from the same species, pollination may not lead to fertilization unless the pollen and stigma belong to genetically distinct individuals. For instance, when pollen from a given plant lands on that plant's own stigma, a pollen tube may begin to develop, but stop before reaching the embryo sac. This **self-incompatibility** is a biochemical recognition and rejection process that prevents self-fertilization, and it apparently results from interactions between proteins encoded by *S* (self) genes.

Research has shown that *S* genes usually have multiple alleles—in some species there may be hundreds—and a common type of incompatibility occurs when pollen and stigma carry an identical *S* allele. The result is a biochemical signal that prevents proper formation of the pollen tube (**Figure 34.7**). For example, studies on plants of the mustard family have revealed that pollen contacting an incompatible stigma produces a protein that prevents the stigma from hydrating the relatively dry pollen grain, an essential step if the pollen tube is to grow. A wide range of self-incompatibility responses has been discovered, however. In cacao, for instance, when incompatible pollen contacts a stigma, a pollen tube grows normally but a hormonal response soon causes the flower to drop off the plant, preventing fertilization.

Self-incompatibility prevents inbreeding and promotes genetic variation, which is the raw material for



**Figure 34.7**  
Self-incompatibility. When a pollen grain has an *S* allele that matches one in the stigma (which is diploid), the result is a biochemical response that prevents fertilization—in this illustration, by preventing the growth of a pollen tube.

natural selection and adaptation. Even so, many flowering plants do self-pollinate, either partly or exclusively, because that mode, too, has benefits in some circumstances. (Mendel's peas are a classic example.) For instance, "selfing" may help preserve adaptive traits in a population. It also reduces or eliminates a plant's reliance on wind, water, or animals for pollination, and thus ensures that seeds will form when conditions for cross-pollination are unfavorable, as when pollinators or potential mates are scarce.

### Double Fertilization Occurs in Flowering Plants

If a pollen grain lands on a compatible stigma, it absorbs moisture and germinates a pollen tube, which burrows through the stigma and style toward an ovule. Chemical cues from the two synergid cells lying close to the egg cell help guide the pollen tube toward its destination. Before or during these events, the pollen grain's haploid sperm-producing cell divides by mitosis, forming two

haploid sperm. When the pollen tube reaches the ovule, it enters through the micropyle and an opening forms in its tip. By this time one synergid has begun to die (an example of programmed cell death), and the two sperm are released into the disintegrating cell's cytoplasm. Experiments suggest that elements of the synergid's cytoskeleton guide the sperm onward, one to the egg cell and the other to the central cell.

Next there occurs a remarkable sequence of events called **double fertilization**, which has been observed only in flowering plants and (in a somewhat different version) in the gnetophyte *Ephedra* (see Section 27.4). Typically, one sperm nucleus fuses with the egg to form a diploid ( $2n$ ) zygote. The other sperm nucleus fuses with the central cell, forming a cell with a triploid ( $3n$ ) nucleus. Tissues derived from that  $3n$  cell are called **endosperm** ("inside the seed"). They nourish the embryo and, in monocots, the seedling, until its leaves form and photosynthesis has begun.

Embryo-nourishing endosperm forms only in flowering plants, and its evolution coincided with a

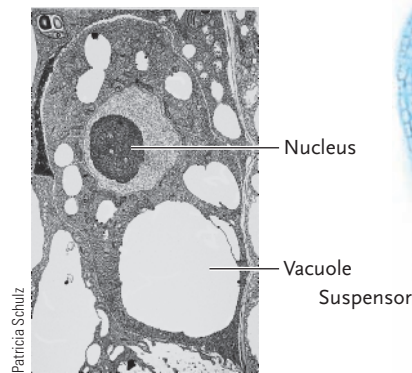
**Figure 34.8**

Stages in the embryonic development of shepherd's purse (*Capsella bursa-pastoris*), a eudicot. Figure 34.16 looks in more detail at the development of early plant embryos. The micrographs are not to the same scale.

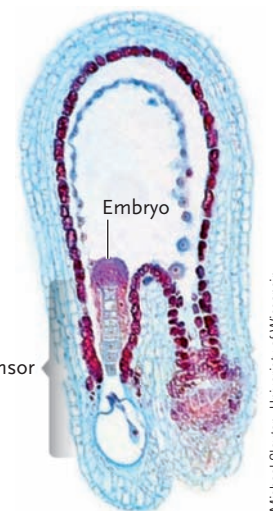
**a.** Shepherd's purse plant (*Capsella bursa-pastoris*)



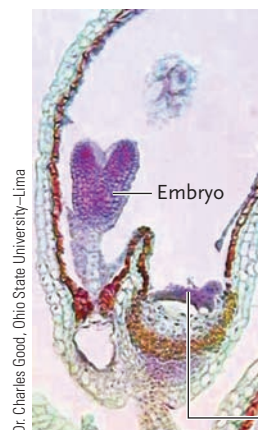
**b.** Zygote, showing the internal organization



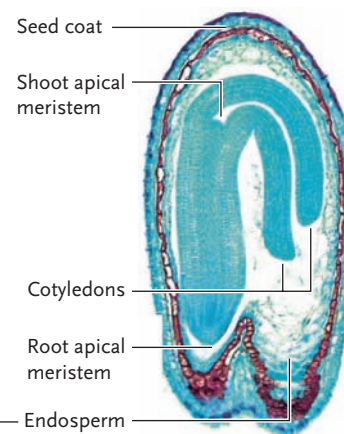
**c.** Globular embryo



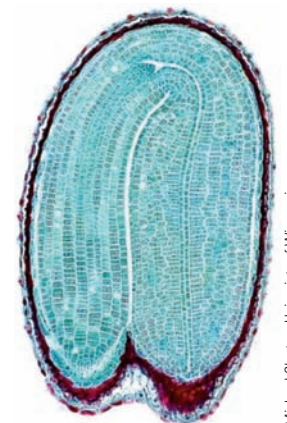
**d.** Heart-shaped embryo



**e.** Well-differentiated embryo



**f.** Embryo sporophyte in mature ovule (the seed)





reduction in the size of the female gametophyte. In other land plants, such as gymnosperms and ferns, the gametophyte itself contains enough stored food to nourish the embryonic sporophytes.

### The Embryonic Sporophyte Develops inside a Seed

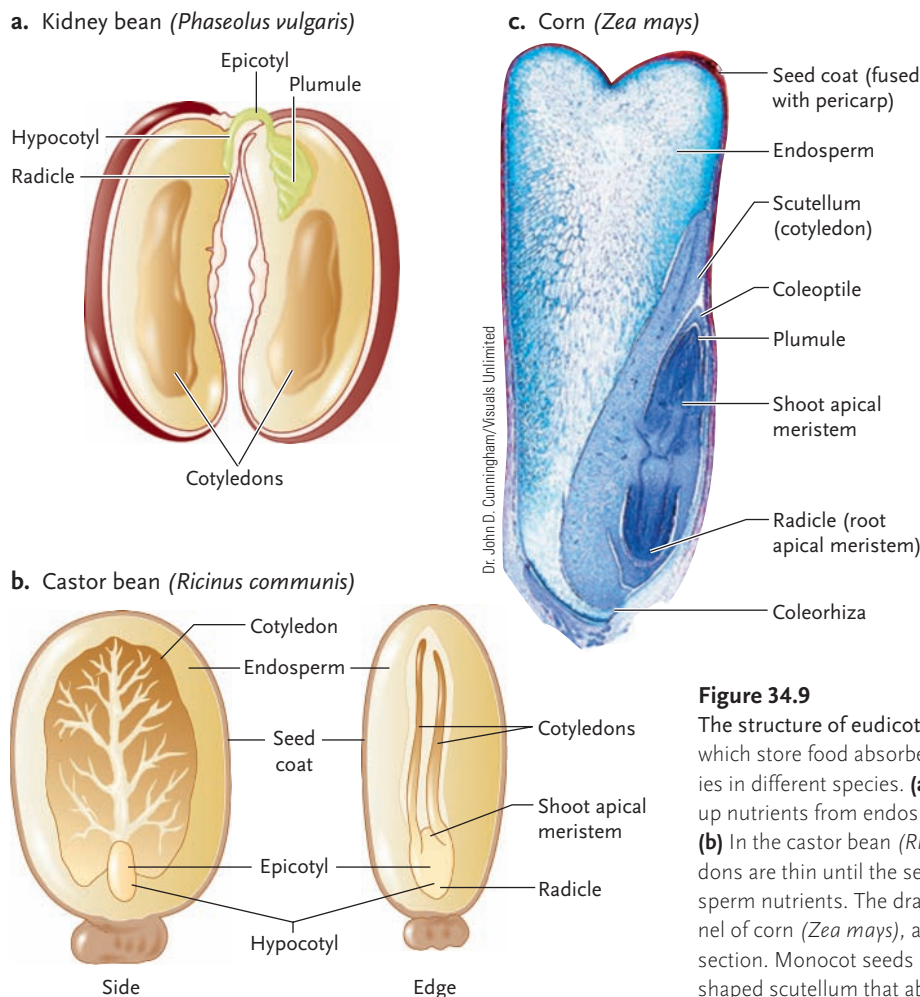
When the zygote first forms, it starts to develop and elongate even before mitosis begins. For example, in shepherd's purse (*Capsella*), shown in **Figure 34.8**, most of the organelles in the zygote, including the nucleus, become situated in the top half of the cell, while a vacuole takes up most of the lower half (see **Figure 34.8b**). The first round of mitosis divides the zygote into an upper *apical cell* and a lower *basal cell*. The apical cell then gives rise to the multicellular embryo, while most descendants of the basal cell form a simple row of cells, the **suspensor**, which transfers nutrients from the parent plant to the embryo (see **Figure 34.8c**).

The first apical cell divisions produce a globe-shaped structure attached to the suspensor. As they continue to grow, embryos of *Capsella* and other eudicots become heart-shaped (see **Figure 34.8d**); each lobe of the “heart” is a developing cotyledon (seed leaf), which provides nutrients for growing tissues. Typically,

the two cotyledons absorb much of the nutrient-storing endosperm and become plump and fleshy. For instance, mature seeds of a sunflower (*Helianthus annuus*) have no endosperm at all. In some eudicots, however, the cotyledons remain as slender structures; they produce enzymes that digest the seed's ample endosperm and transfer the liberated nutrients to the seedling. Monocots have one, large cotyledon; in many monocot species, especially grasses such as corn and rice, the cotyledon absorbs the endosperm after germination, when the embryo inside the seed begins to grow.

By the time the ovule is mature—that is, a fully developed seed—it has become encased by a protective **seed coat**. Inside the seed, the sheltered embryo has a lengthwise axis with a root apical meristem at one end and a shoot apical meristem at the other (see **Figure 34.8e, f**).

**Figure 34.9a** and **Figure 34.9b** illustrate the structure of the seeds of two eudicots, the kidney bean (*Phaseolus vulgaris*) and the castor bean (*Ricinus communis*). The kidney bean has broad, fleshy cotyledons and the castor bean much thinner ones, but in other ways the embryos are quite similar. The **radicle**, or embryonic root, is located near the micropyle, where the pollen tube entered the ovule prior to fertilization. The radicle



**Figure 34.9**

The structure of eudicot and monocot seeds. Eudicot seeds have two cotyledons, which store food absorbed from the endosperm, but the timing of this function varies in different species. **(a)** The cotyledons of a kidney bean (*Phaseolus vulgaris*) take up nutrients from endosperm while the seed develops, becoming plump and fleshy. **(b)** In the castor bean (*Ricinus communis*), the endosperm is thick and the cotyledons are thin until the seed germinates, when the cotyledons begin to take up endosperm nutrients. The drawing on the right gives a side view of the embryo. **(c)** A kernel of corn (*Zea mays*), a representative monocot seed, shown here in longitudinal section. Monocot seeds have a single cotyledon, which develops into a shield-shaped scutellum that absorbs nutrients from endosperm.

attaches to the cotyledon at a region of cells called the **hypocotyl**. Beyond the hypocotyl is the **epicotyl**, which has the shoot apical meristem at its tip and which often bears a cluster of tiny foliage leaves, the **plumule**. At germination, when the root and shoot first elongate and emerge from the seed, the cotyledons are positioned at the first stem node with the epicotyl above them and the hypocotyl below them.

The embryos of monocots such as corn differ structurally from those of eudicots in several ways (**Figure 34.9c**). They have only one very large cotyledon, called a **scutellum**. In addition, the root and shoot apical meristems of monocots are blanketed by protective tissues. The shoot apical meristem and plumule are covered by a **coleoptile**, a sheath of cells that protects them during upward growth through the soil. A similar covering, the **coleorhiza**, sheathes the radicle until it breaks out of the seed coat and enters the soil as the primary root. The actual embryo of a corn plant is buried deep within the corn “kernel,” which technically is called a *grain*. Most of the moist interior of a fresh corn grain is endosperm; the single cotyledon forms a plump, shield-shaped mass that absorbs nutrients from the endosperm.

### Fruits Protect Seeds and Aid Seed Dispersal

Most angiosperm seeds are housed inside fruits, which provide protection and often aid seed dispersal. A **fruit** is a matured or ripened ovary. Usually, fruits begin to develop after a flower’s ovule or ovules are fertilized by pollen, and the start of ovule growth after pollination is called “fruit set.” The fruit wall, called the **pericarp**, develops from the ovary wall and can have several layers. Hormones in pollen grains provide the initial stimulus that turns on the genetic machinery leading to fruit development; additional signals come from hormones produced by the developing seeds.

Fruits are extremely diverse, and biologists classify them into types based on combinations of structural features. A major defining feature is the nature of the pericarp, which may be fleshy (as in peaches) or dry (as in a hazelnut). A fruit also is classified according to the number of ovaries or flowers from which it develops. **Simple fruits**, such as peaches, tomatoes, and the cacao fruits pictured in Figure 34.1, develop from a single ovary, and in many of them at least one layer of the pericarp is fleshy and juicy. Other simple fruits, including grains and nuts, have a thin, dry pericarp, which may be fused to the seed coat. The garden pea (*Pisum sativa*) is a simple fruit, the peas being the seeds and the surrounding shell the pericarp. **Aggregate fruits** are formed from several ovaries in a single flower. Examples are raspberries and strawberries, which develop from clusters of ovaries. Strawberries also qualify as *accessory* fruits, in which floral parts in addition to the ovary become incorporated as the fruit develops. For instance, anatomically, the fleshy part of a straw-

berry is an expanded receptacle (the end of the floral shoot) and the strawberry fruits are the tiny, dry nubbins (called *achenes*) you see embedded in the fleshy tissue of each berry. **Multiple fruits** develop from several ovaries in multiple flowers. For example, a pineapple is a multiple fruit that develops from the enlarged ovaries of several flowers clustered together in an inflorescence. **Figure 34.10** shows examples of some different types of fruits.

Fruits have two functions: they protect seeds, and they aid seed dispersal in specific environments. For example, the shell of a sunflower seed is a pericarp that protects the seeds within. A pea pod is a pericarp that in nature splits open to disperse the seeds (peas) inside. Maple fruits have winglike extensions for dispersal (see Figure 34.10e). When the fruit drops, the wings cause it to spin sideways and also can carry it away on a breeze. This aerodynamic property propels maple seeds to new locations, where they will not have to compete with the parent tree for water and minerals. Fruits also may have hooks, spines, hairs, or sticky surfaces, and they are ferried to new locations when they adhere to feathers, fur, or blue jeans of animals that brush against them. Fleshy fruits such as blueberries and cherries are nutritious food for many animals, and their seeds are adapted for surviving digestive enzymes in the animal gut. The enzymes remove just enough of the hard seed coats to increase the chance of successful germination when the seeds are expelled from the animal’s body in feces.

### Seed Germination Continues the Life Cycle

A mature seed is essentially dehydrated. On average, only about 10% of its weight is water—too little for cell expansion or metabolism. After a seed is dispersed and germinates, the embryo inside it becomes hydrated and resumes growth. Ideally, a seed germinates when external conditions favor the survival of the embryo and growth of the new sporophyte. This timing is important, for once germination is underway the embryo loses the protection of the seed coat and other structures that surround it. Overall, the amount of soil moisture and oxygen, the temperature, day length, and other environmental factors influence when germination takes place.

In some species, the life cycle may include a period of seed **dormancy** (*dormire* = to sleep), in which biological activity is suspended. Botanists have described a striking array of variations in the conditions required for dormant seeds to germinate. For instance, seeds may require minimum periods of daylight or darkness, repeated soaking, mechanical abrasion, or exposure to certain enzymes, the high heat of a fire, or a freeze–thaw cycle before they finally break dormancy. In some desert plants, hormones in the seed coat inhibit growth of a seedling until heavy rains flush them away. This adaptation prevents seeds from germinating unless there is

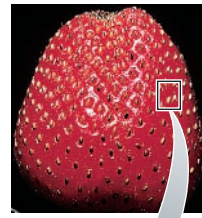
a. Peach (*Prunus*), a simple fruit    b. Raspberry (*Rubus*), an aggregate fruit



Fleshy pericarp



c. Strawberry (*Fragaria*), an accessory fruit



Richard H. Gross



Fruit wall

Siegel, R./Arco Images/Peter Arnold, Inc.

Andrew Syred/SPL/Photo Researchers, Inc.

d. Pineapple (*Ananas comosus*), a multiple fruit



One of many individual fruits



R. Carr

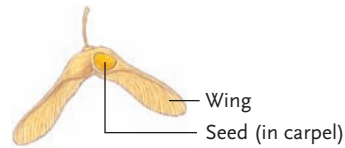


Figure 34.10

Fruits. (a) Peach, a fleshy simple fruit. (b) Raspberry (*Rubus*), an aggregate fruit. (c) Strawberry (*Fragaria ananassa*), an accessory fruit that is also an aggregate fruit. (d) Pineapple (*Ananas comosus*), a multiple fruit. (e) Winged fruits of maple (*Acer*).

enough water in the soil to support growth of the plant through the flowering and seed production stages before the soil dries once again. Many desert plants—and plants in harsh environments such as alpine tundra—cycle from germination to growth, flowering, and seed development in the space of a few weeks, and their offspring remain dormant as seeds until conditions once again favor germination and growth.

Seeds of some species appear to remain viable for amazing lengths of time. Thousand-year-old lotus seeds (*Nelumbo lutea*) discovered in a dry lake bed have germinated trouble-free. And in one startling case, seeds of arctic lupine (*Lupinus arcticus*) were discovered in the 10,000-year-old frozen entrails of a lemming. When they were thawed, they readily germinated as well.

Germination begins with **imbibition**, in which water molecules move into the seed, attracted to hydrophilic groups of stored proteins. As water enters, the seed swells, the coat ruptures, and the radicle begins

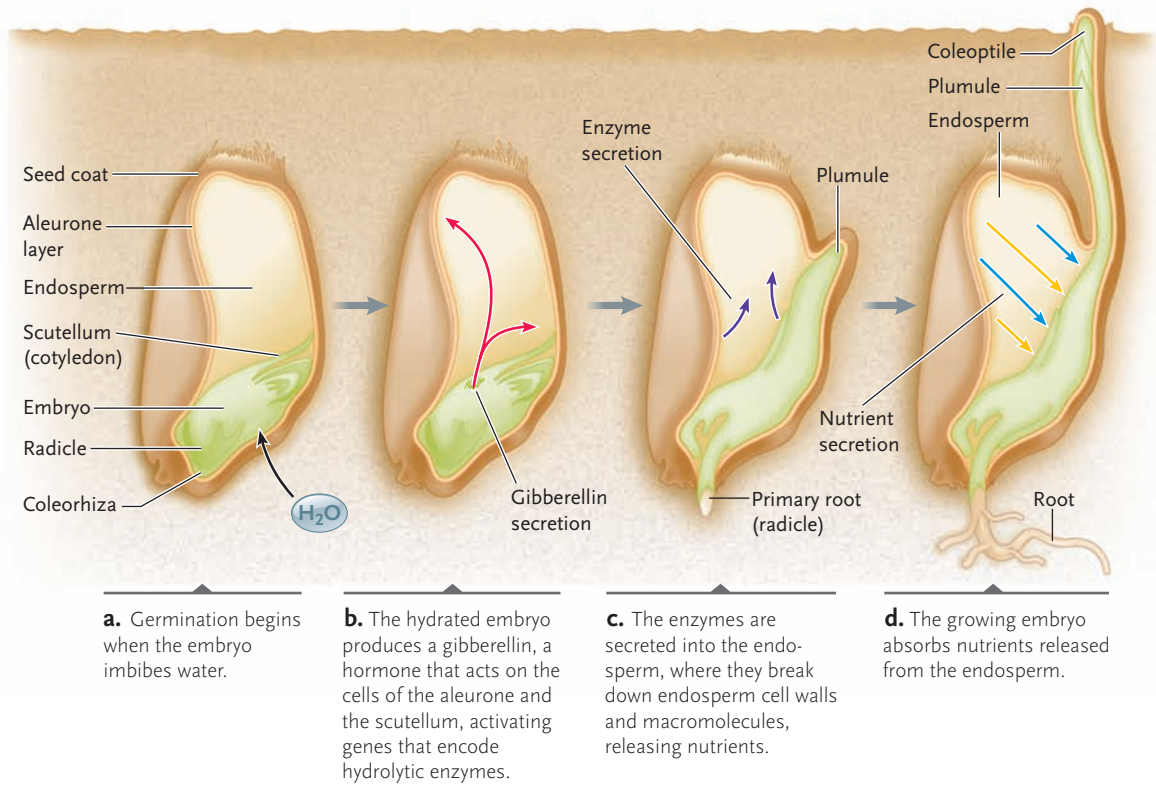
its downward growth into the soil. Within this general framework, however, there are many variations among plants.

Once the seed coat splits, water and oxygen move more easily into the seed. Metabolism switches into high gear as cells divide and elongate to produce the seedling. Stable enzymes that were synthesized before dormancy become active; other enzymes are produced as the genes encoding them begin to be expressed. Among other roles, the increased gene activity and enzyme production mobilize the seed's food reserves in cotyledons or endosperm. Nutrients released by the enzymes sustain the rapidly developing seedling until its root and shoot systems are established.

The events of seed germination have been studied extensively in cereal grains, and **Figure 34.11** illustrates them in barley. Notice that the seed's endosperm is separated from the pericarp by a thin layer of cells called the **aleurone**. As a hydrating seed imbibes water, the embryo produces a *gibberellin*, a hormone that

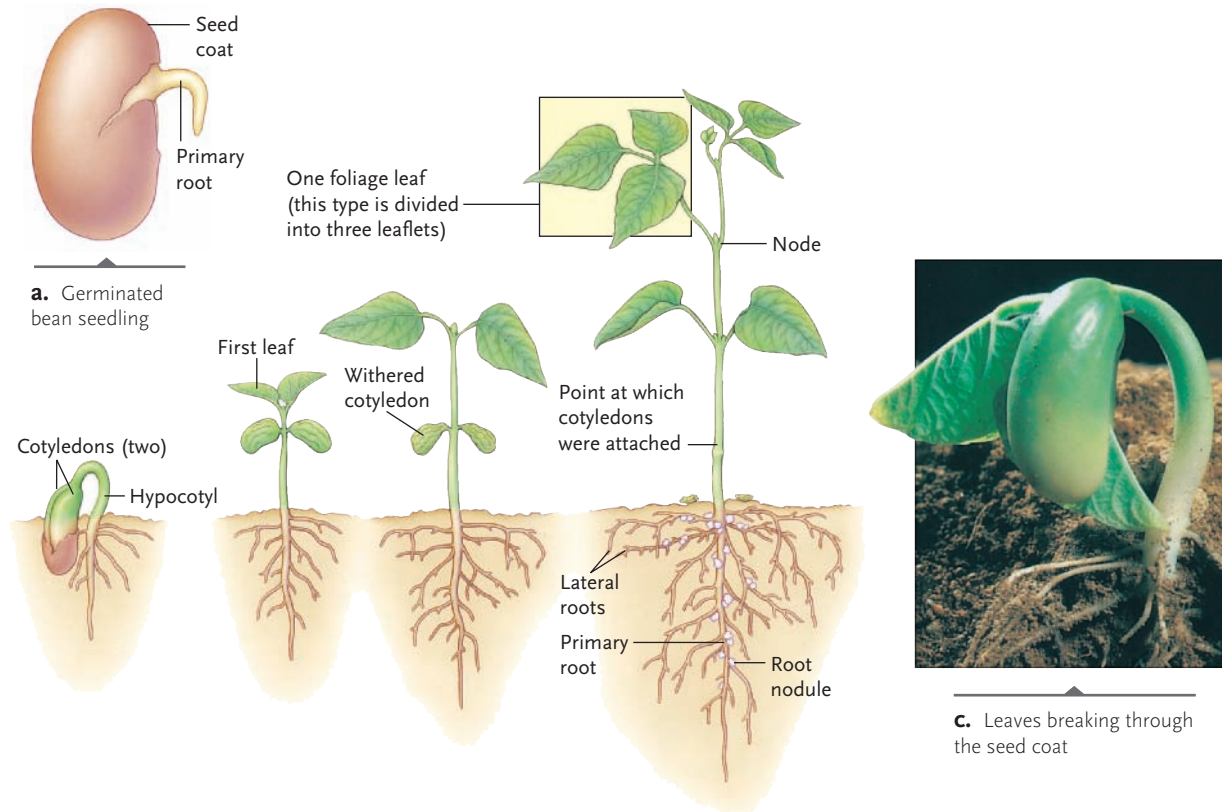
**Figure 34.11**

How food reserves are mobilized in a germinated seed of barley (*Hordeum vulgare*), a monocot.

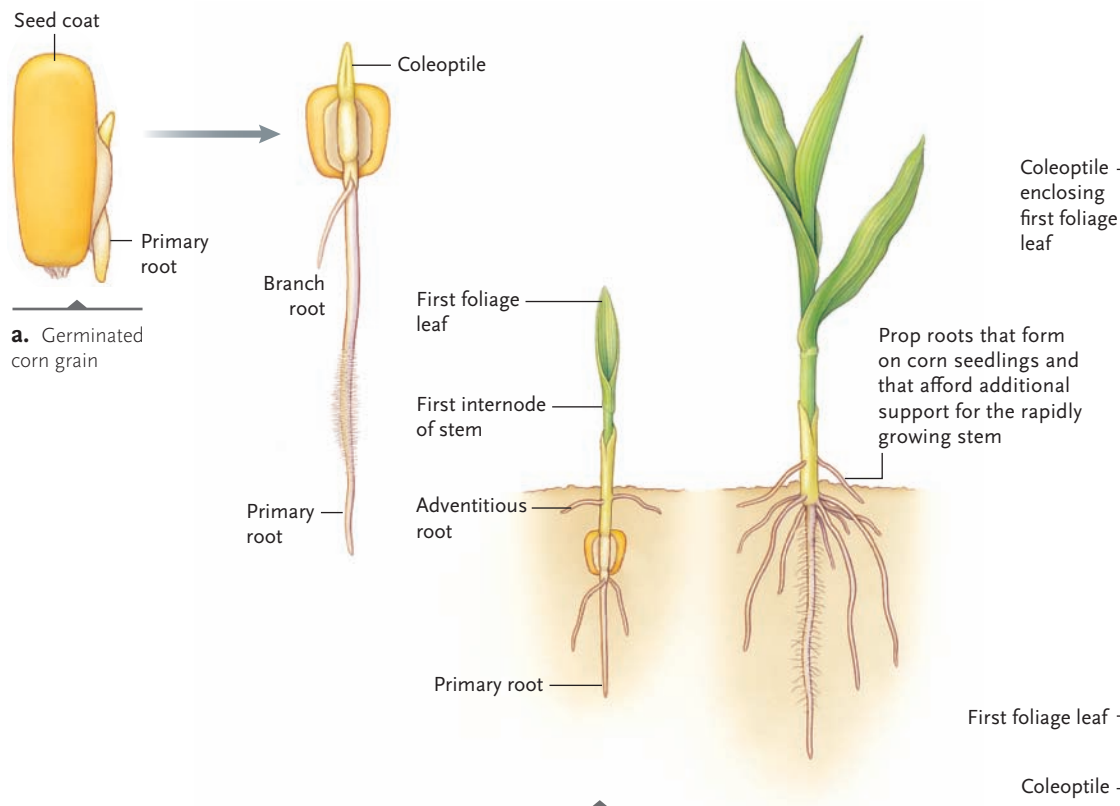


**Figure 34.12**

Stages in the development of a representative eu-dicot, the kidney bean (*Phaseolus vulgaris*).



Herve Chaumetoni/Agence Nature



a. Germinated corn grain

Primary root

Primary root

First foliage leaf

First internode of stem

Adventitious root

Primary root

Prop roots that form on corn seedlings and that afford additional support for the rapidly growing stem

Coleoptile enclosing first foliage leaf



c. Coleoptile and primary root



First foliage leaf

Coleoptile

d. Coleoptile and first foliage leaf of two seedlings breaking through the soil surface

b. The young leaves are enclosed in a coleoptile, which protects them during upward growth through the soil. Adventitious roots develop from the first node at the base of the coleoptile. When a grain is planted deep, the first internode elongates, separating the primary and adventitious roots. When a grain is planted close to the soil surface, light inhibits elongation of the first internode and the primary and adventitious roots look as if they originate in the same region of the stem.

stimulates aleurone cells to manufacture and secrete hydrolytic enzymes. Some of these enzymes digest components of endosperm cell walls; others digest proteins, nucleic acids, and starch of the endosperm, releasing nutrient molecules for use by cells of the young root and shoot. Although it is clear that nutrient reserves are also mobilized by metabolic activity in eudicots and in gymnosperms, the details of the process are not well understood.

Inside a germinating seed, embryonic root cells are generally the first to divide and elongate, giving rise to the radicle. When the radicle emerges from the seed coat as the primary root, germination is complete. **Figure 34.12** and **Figure 34.13** depict the stages of early development in a kidney bean, a eudicot, and in corn, a monocot. As the young plant grows, its development continues to be influenced by interactions of hormones and environmental factors, as you will read in Chapter 35.

Most plants give rise to large numbers of seeds because, in the wild, only a tiny fraction of seeds survive, germinate, and eventually grow into another mature plant. Also, flowers, seeds, and fruits represent major investments of plant resources. Asexual reproduction, discussed next, is a more “economical” means by which many plants can propagate themselves.

## STUDY BREAK

1. Explain the sequence of events in a flowering plant that begins with formation of a pollen tube and culminates with the formation of a diploid zygote and the  $3n$  cell that will give rise to endosperm in a seed.
2. Early angiosperm embryos undergo a series of general changes as a seed matures. Summarize this sequence, then describe the structural differences that develop in the seeds of monocots and eudicots.
3. Germination begins when a seed imbibes water. What are the next key biochemical and developmental events that bring an angiosperm’s life cycle full circle?

## 34.4 Asexual Reproduction of Flowering Plants

As noted in Chapter 31, nodes in the stolons of strawberries and the rhizomes of Bermuda grass each can give rise to new individuals. So can “suckers” that

**Figure 34.13** Stages in the development of a representative monocot, the corn plant (*Zea mays*).

sprout from the roots of blackberry bushes and “eyes” in the tubers of potatoes. All these examples involve asexual or **vegetative reproduction** from a nonreproductive plant part, usually a bit of meristematic tissue in a bud on the root or stem. All of them produce offspring that are clones of the parent. Vegetative reproduction relies on an intriguing property of plants—namely, that many fully differentiated plant cells are **totipotent** (“all powerful”). That is, they have the genetic potential to develop into a whole, fully functional plant. Under appropriate conditions, a totipotent cell can *dedifferentiate*: it returns to an unspecialized embryonic state, and the genetic program that guides the development of a new individual is turned on.

### Vegetative Reproduction Is Common in Nature

Various plant species have developed different mechanisms for reproducing asexually. In the type of vegetative reproduction called **fragmentation**, cells in a piece of the parent plant dedifferentiate and then can regenerate missing plant parts. Many gardeners have discovered to their frustration that a chunk of dandelion root left in the soil can rapidly grow into a new dandelion plant in this way.

When a leaf falls or is torn away from a jade plant (*Crassula* species), a new plant can develop from meristematic tissue in the detached leaf adjacent to the wound surface. In the “mother of thousands” plant, *Kalanchoe daigremontiana*, meristematic tissue in notches along the leaf margin gives rise to tiny plantlets (**Figure 34.14**) that eventually fall to the ground, where they can sprout roots and grow to maturity.

Some flowering plants, including some citrus species and the grass variety known as Kentucky blue grass (*Poa pratensis*), can reproduce asexually through a mechanism called **apomixis**. Typically, a diploid embryo develops from an unfertilized egg or from diploid

cells in the ovule tissue around the embryo sac. The resulting seed is said to contain a **somatic embryo**, which is genetically identical to the parent.

In wild plant species, most types of asexual reproduction result in offspring located near the parent. These clonal populations lack the variability provided by sexual reproduction, variation that enhances the odds for survival when environmental conditions change. Yet asexual reproduction offers an advantage in some situations. It usually requires less energy than producing complex reproductive structures such as seeds and showy flowers to attract pollinators. Moreover, clones are likely to be well suited to the environment in which the parent grows.

### Many Commercial Growers and Gardeners Use Artificial Vegetative Reproduction

For centuries, gardeners and farmers have used asexual plant propagation to grow particular crops and trees and some ornamental plants. They routinely use *cuttings*, pieces of stems or leaves, to generate new plants; placed in water or moist soil, a cutting may sprout roots within days or a few weeks. Trees and wine grapes often are propagated by grafting a bud or branch from a plant with desirable fruit traits—the *scion*—and joining it to a root or stem from a plant with useful root traits—the *stock*. A grafted plant usually produces flowers and fruit identical to those of the scion’s parent plant. The scion of a grafted wine grape variety may be chosen for the quality of its fruit and the stock for its hardy, disease-resistant root system. Vegetative propagation can also be used to grow plants from single cells. Rose bushes and fruit trees from nurseries and commercially important fruits and vegetables such as Bartlett pears, McIntosh apples, Thompson seedless grapes, and asparagus come from plants produced vegetatively in tissue culture conditions that cause their cells to dedifferentiate to an embryonic stage.

**Vegetative Propagation in Tissue Culture.** In groundbreaking experiments in the 1950s, Frederick C. Steward explored the totipotency of plant cells. Together with his coworkers at Cornell University, Steward propagated whole carrot plants in the laboratory by culturing carrot root phloem. Later researchers confirmed that almost any plant cell that has a nucleus and lacks a secondary cell wall may be totipotent.

The method of plant tissue culture Steward pioneered is simple in its general outlines (**Figure 34.15**). Bits of tissue are excised from a plant and grown in a nutrient medium. The procedure disrupts normal interactions between cells in the tissue sample, and the cells dedifferentiate and form an unorganized, white cell mass called a **callus**. When cultured with nutrients and growth hormones, some cells of the callus regain

**Figure 34.14**  
*Kalanchoe daigremontiana*, the mother-of-thousands plant. Each tiny plant growing from the leaf margin can become a new, independent adult plant.



Ed Reschke/Peter Arnold, Inc.

totipotency and develop into plantlets with roots and shoots.

Steward's work laid the foundation for large-scale commercial applications of plant tissue culture, as well as for a whole new field of research on *somatic embryogenesis* in plants. Single cells derived from a callus generated from shoot meristem are placed in a medium containing nutrients and hormones that promote cell differentiation. With some species, totipotent cells in the sample eventually give rise to diploid somatic embryos that can be packaged with nutrients and hormones in artificial “seeds” (see Figure 34.15). Endowed with the same traits as their parent, crop plants grown from somatic embryos are genetically uniform.

However, mutations often occur in the DNA of somatic embryos derived from callus culture. Screening techniques can identify such *somaclonal* mutants with desirable traits—for example, resistance to a disease that attacks wild-type plants of the same species. In plants that are infected with viruses, callus cultures can be restricted to virus-free cells and thus generate virus-free clones. Tissue culture propagation can then produce hundreds or thousands of identical plants from a single specimen. This technique, called **somaclonal selection**, is now a staple tool in efforts to improve major food crops, such as corn, wheat, rice, and soybeans. It is also being used to rapidly increase stocks of hybrid orchids, lilies, and other valued ornamental plants. The yellow and orange tomatoes that have become common in produce markets are the fruits of plants developed by somaclonal selection.

Research on tobacco and some other species has shown that plants can also be regenerated by **protoplast fusion**. In this method, the walls of living cells in solution are first digested away by enzymes, leaving the protoplasts. Then the protoplasts are induced to fuse, either by applying an electric current, a laser beam, or chemical additives to the solution, which briefly “loosen” the plasma membranes. The resulting cell (now  $4n$ , or tetraploid) is transferred to a solid nutrient medium and allowed to develop into a callus; then individual callus cells are stimulated to develop into embryos. If the fused protoplasts come from somatic cells of a single species, the embryos often grow into fertile plants. It has proven more difficult to grow fertile hybrids from fused protoplasts of different species and genera, probably because there are species-specific signals that govern key physiological functions. Even so, this method has produced the pomato, a cross between a potato and a tomato.

Regardless of how it comes into being, an embryonic sporophyte changes significantly as it begins the developmental journey toward maturity, when it will be capable of reproducing. Next we explore what researchers are learning about these developmental changes.

## STUDY BREAK

1. Describe three modes of asexual reproduction that occur in flowering plants.
2. What is totipotency, and how do methods of tissue culture exploit this property of plant cells?

## 34.5 Early Development of Plant Form and Function

Unlike animals, plants have specialized body parts such as leaves and flowers that may arise from meristems throughout an individual's life—sometimes for thousands of years. Accordingly, in plants the biological role of embryonic development is not to generate the tissues and organs of the adult, but to establish a basic body plan—the root–shoot axis and the radial, “outside-to-inside” organization of epidermal, ground, and vascular tissues (see Section 31.1)—and the precursors of the primary meristems. Though they may sound simple, these fundamentals and the stages beyond them all require an intricately orchestrated sequence of molecular events that plant scientists are defining through sophisticated experimentation.

One of the most fruitful approaches has been the study of plants with natural or induced gene mutations that block or otherwise affect steps in development—and accordingly lend insight into the developmental roles of the normal, wild-type versions of those abnormal genes. Some of these genes are **homeotic genes**, regulatory genes in the genome of an organism that encode transcription factors. The transcription factors are proteins that control the expression of other genes, which in turn direct events in development (see *Focus on Research* in Chapter 31). While researchers work with various species to probe the genetic underpinnings of early plant development, the thale cress (*Arabidopsis thaliana*) has become a favorite model organism for plant genetic research (see *Focus on Research*).

### Within Hours, an Early Plant Embryo's Basic Body Plan Is Established

The entire *Arabidopsis* genome has been sequenced, providing a powerful molecular “database” for determining how various genes contribute to shaping the plant body. Experimenters' ability to trace the expression of specific genes has shed considerable light on how the root–shoot axis is set and how the three basic plant tissue systems arise.

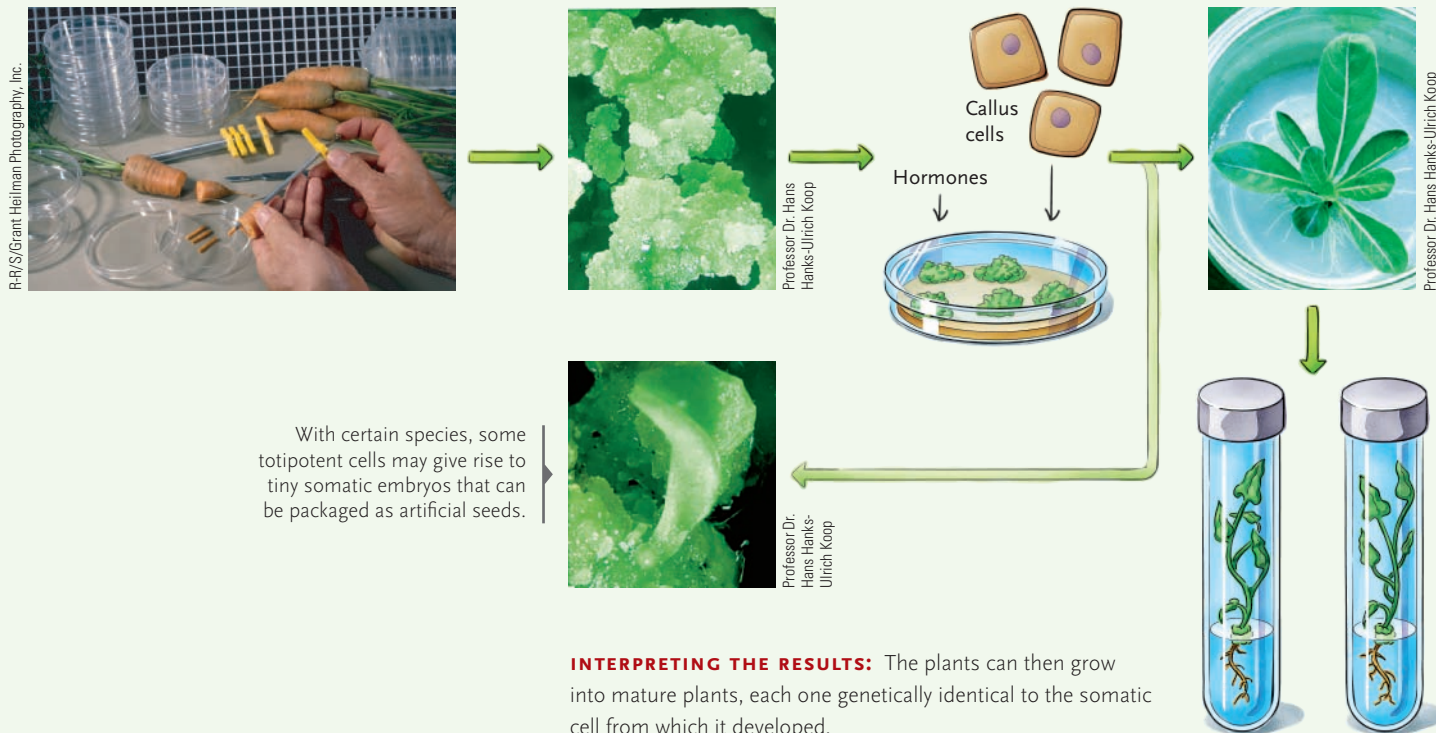
**The Root–Shoot Axis.** Shortly after fertilization gives rise to an *Arabidopsis* zygote, the single cell divides. Electron microscopy shows that, as with the *Capsella*

## Figure 34.15 Research Method

### Plant Cell Culture

#### PROTOCOL:

1. Typically, bits of somatic tissue are excised, often from root and shoot tips or meristems, because these parts tend to be free of viruses. The excised tissue is cultured in a nutrient medium, under strictly controlled environmental conditions.
2. Within a few days, cells in the excised tissue dedifferentiate and form an unorganized tissue mass called a callus.
3. Individual callus cells can be separated out and cultured in a medium containing growth hormones.
4. Totipotent cells eventually give rise to plantlets with roots and shoots.



**INTERPRETING THE RESULTS:** The plants can then grow into mature plants, each one genetically identical to the somatic cell from which it developed.

zygote described earlier, this first round of mitosis produces a small apical cell and a larger basal cell (**Figure 34.16a**). The apical cell receives the lion's share of the cytoplasm, while the basal cell receives the zygote's large vacuole and less cytoplasm. Researchers have confirmed that this asymmetrical division of the zygote results in the daughter cells receiving different mixes of mRNAs—the gene transcripts that will be translated into proteins.

Translation of differing mRNAs produces proteins that include several transcription factors, and it marks the genetic threshold of the separation of the plant body into root and shoot regions. As transcription factors trigger the expression of differing genes, distinct biochemical pathways unfold in sequence in the two cells. For example, a basal cell initially exports a signaling molecule (a hormone of the auxin family, discussed in Chapter 35) to the apical cell, and this sets in motion steps leading to the development of the various embryonic shoot features. Later, gene expression

and the flow of chemical signals shift in ways that promote the development of specific structures from the basal cell, including portions of the root apical meristem.

Several of the genes that influence root–shoot polarity have been identified, and when any of them is disrupted, the result can be a serious defect. For example, when an embryo receives two copies of a mutant gene called *gnom*, the embryo doesn't develop distinct root and shoot regions. Instead it remains a lumpy blob (**Figure 34.16b**).

**Radial Organization of Tissue Layers.** A day or so after an *Arabidopsis* egg cell is fertilized, the embryo consists of eight cells. Even at this early stage both the root–shoot axis and the beginnings of tissue systems are present. When an embryo reaches the so-called torpedo stage, cells representing all three basic tissue systems are in place (**Figure 34.16c**). Again working with mutant plants, investigators have identified





## FOCUS ON RESEARCH

### Model Research Organisms: *Arabidopsis thaliana*

For plant geneticists, the little white-flowered thale cress, *Arabidopsis thaliana*, has attributes that make it a prime subject for genetic research. A tiny member of the mustard family, *Arabidopsis* is revealing answers to some of the biggest questions in plant development and physiology.

Each plant grows only a few centimeters tall, so little laboratory space is required to house a large population. As long as *Arabidopsis* is provided with damp soil containing basic nutrients, it grows easily and rapidly in artificial light. Like Mendel's peas, *Arabidopsis* is self-compatible and self-fertilizing, and the flowers of a single plant can yield thousands of seeds per mating. Seeds grow to mature plants in just over a month and then flower and reproduce themselves in another 3 to 4 weeks. This permits investigators to perform desired genetic crosses and obtain large numbers of offspring having known, desired genotypes with

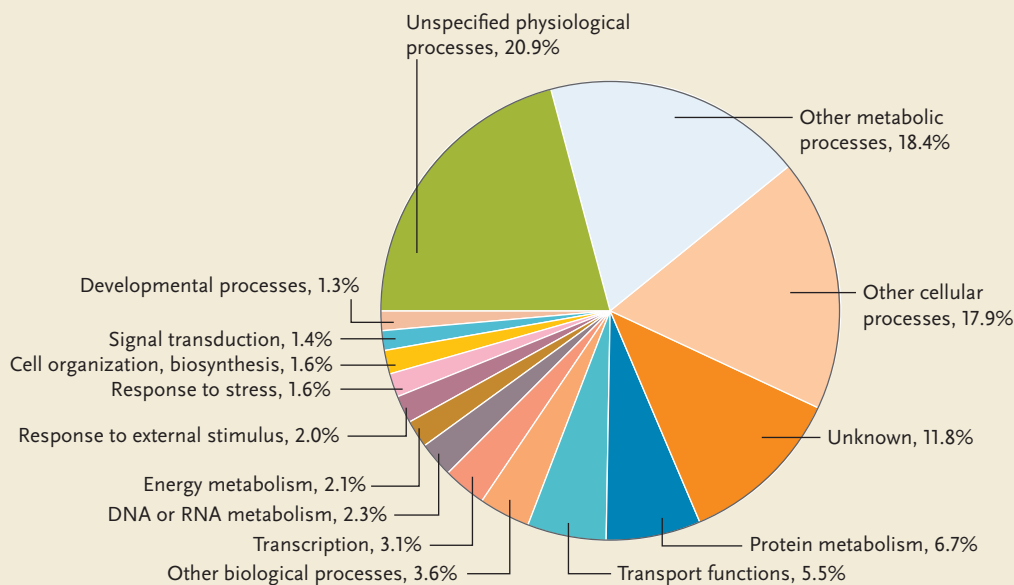
relative ease. Individual *Arabidopsis* cells also grow well in culture.

The *Arabidopsis* genome was the first complete plant genome to be sequenced; at this writing researchers have identified approximately 28,000 genes arranged on five pairs of chromosomes. The genome contains relatively little repetitive DNA, so it is fairly easy to isolate *Arabidopsis* genes, which can then be cloned using genetic engineering techniques. Cloned genes are inserted into bacterial plasmids and the recombinant plasmids transferred to the bacterial species *Agrobacterium tumefaciens*, which readily infects *Arabidopsis* cells. Amplified by the bacteria, the genes and their protein products can be sequenced or studied in other ways.

Typically, researchers use chemical mutagens or recombinant bacteria to introduce changes in the *Arabidopsis* genome. These mutants have become powerful tools for exploring molecular

and cellular mechanisms that operate in plant development—for example, elucidation of the homeotic genes responsible for flower development described in this chapter. *Arabidopsis* mutants are also being used to probe fundamental questions such as how plant cells respond to gravity and the role of pigments called phytochromes in plant responses to light.

An ambitious, multinational research effort called the 2010 Project aims to determine the functions of all *Arabidopsis* genes by 2010. The Arabidopsis Information Resource (TAIR) recently estimated the percentages of *A. thaliana* genes in different functional categories (**Figure a**). The goal of Project 2010 is to create a comprehensive genetic portrait of a flowering plant—how each gene affects the functioning of not only individual cells but the plant as a whole.



**Figure a**

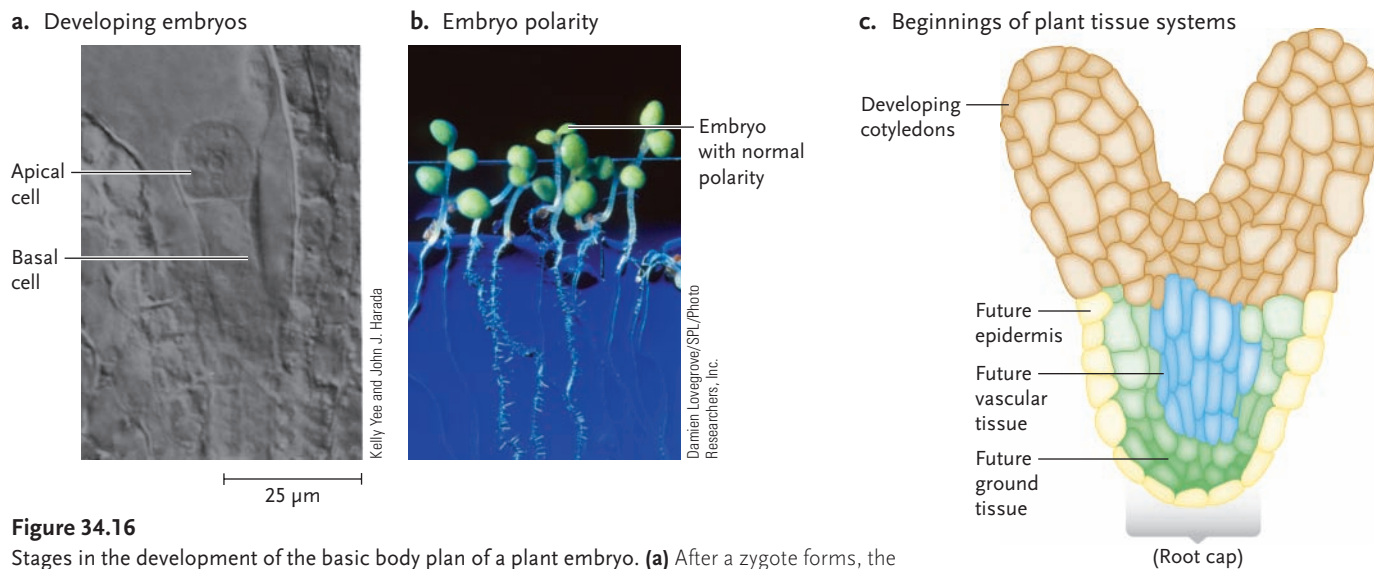
The percentages of *A. thaliana* genes that influence different functional categories.

(Courtesy of the Arabidopsis Information Resource, 2005.)



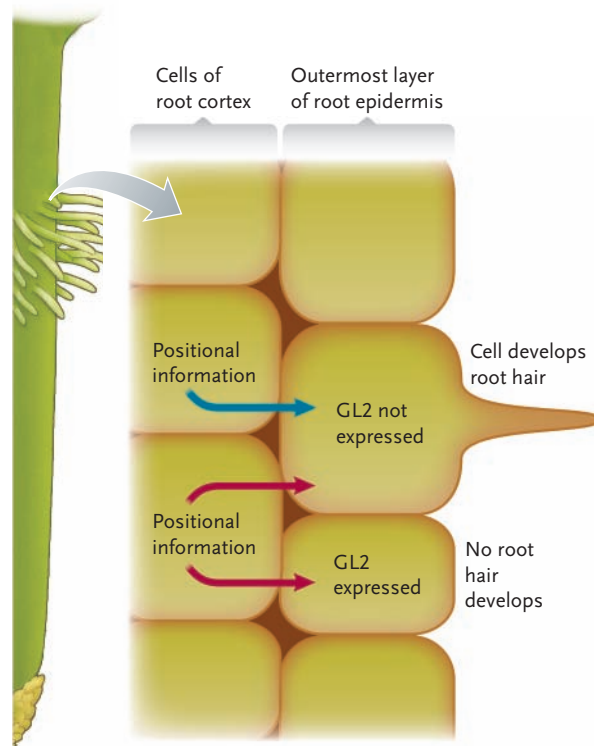
several *Arabidopsis* genes that help govern early development of tissue systems. For example, a gene called *SCR* encodes a protein that apparently regulates mitotic divisions that produce the first cells of a developing root's cortex and endoderm tissue layers (Figure 31.20 shows the locations of these tissues in a mature root). The roots of a mutant *scr* seedling contain cells with jumbled characteristics of both tissue layers.

No matter what the species, nearly all new plant embryos have the general body plan we have been discussing. As development proceeds, cells at different sites become specialized in prescribed ways as a particular set of genes is expressed in each type of cell—a process known as *differentiation*. Differentiated cells in turn are the foundation of specialized tissues and organs, which come about through processes we consider next.



**Figure 34.16**

Stages in the development of the basic body plan of a plant embryo. **(a)** After a zygote forms, the first round of cell division produces an embryo with an apical cell that contains much of the zygote's cytoplasm, and a larger basal cell that receives the vacuole and less cytoplasm. The division allots different transcription factors to each cell and establishes the plant's root–shoot axis. **(b)** Normal *A. thaliana* seedlings, in which the root–shoot polarity has become established. **(c)** The approximate locations of early embryonic cells that are the forerunners of epidermal, ground, and vascular tissue systems, respectively.



**Figure 34.17**

One model of how positional information influences the development of root hairs. In this model, the only epidermal cells that develop root hairs are those whose inner wall is in contact with two root cortex cells. Such positioning gives rise to signals that block the expression of the GL2 (GLABRA2) gene. When GL2 is expressed, a root epidermal cell will not develop a root hair.

### Key Developmental Cues Are Based on a Cell's Position

Although many of the specifics of development differ in animals and plants, one fundamental holds true for both: Normal development produces ordered spatial arrangements of differentiated tissues. Examples in plants include root and shoot apical meristems at opposite ends of the root–shoot axis, the cotyledons that divide the shoot into an upper epicotyl and a lower hypocotyl, and the nested layers of vascular, ground, and epidermal tissue systems. Developmental biologists call this progressive ordering of parts **pattern formation**, and a wealth of research has shown that it is guided by the position of cells relative to one another. Such *positional information* helps establish a cell's developmental fate: that is, it provides cues that “tell” cells where they are in the developing embryo and thus lay the groundwork for an appropriate genetic response.

Numerous researchers have explored how cells in a developing plant or plant part receive and respond to positional information. Experiments have demonstrated, for example, that only certain cells in the epidermis of an embryonic root will give rise to root hairs, the type of trichomes that take up water and minerals from soil (see Section 31.2). These specialized root epidermal cells all share the same position with respect to the underlying root cortex—each abuts two cortical cells. By contrast, no root hair extension will develop from an epidermal cell that lines up against only one cortical cell. **Figure 34.17** diagrams one model of what happens next. In this scenario, one or more

## INSIGHTS FROM THE MOLECULAR REVOLUTION

### Trichomes: Window on Development in a Single Plant Cell

The delicate plant cell extensions called trichomes are helping to illuminate developmental processes that go on in a single plant cell as it differentiates—that is, as it acquires its ultimate specialized structure and function. In *Arabidopsis* each of these minute protuberances consists of a single cell with a branching tripartite pattern (**Figure a**).

A curious feature of trichomes is that as one differentiates, increases in size, and extends branches in different directions, its chromosomes—and the cell's DNA—and duplicated several times over without mitosis (a process

called endoreduplication). As a result, the cell has multiple copies of chromosomes. Experiments that isolate the effects of different mutants have helped confirm that the amount of DNA in the cell strongly influences the cell's structure, and that several genes interact to determine it. One of these genes is called *TRY* (for *TRIPTYCHON*); when it is mutated the affected plant's trichomes have a double complement of DNA and develop five branches (**Figure b**). But genes that regulate the cell cycle are only part of the story. Experiments with other mutants show that several other genes also help produce

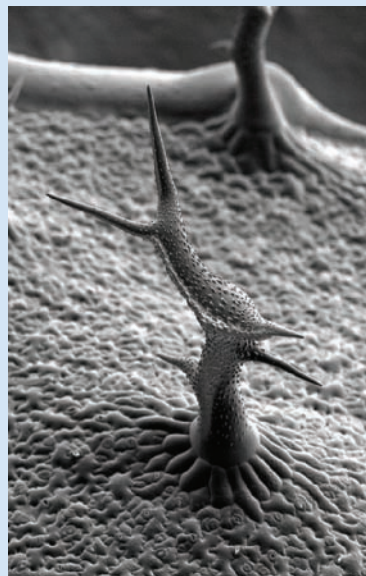
the characteristic three-pronged trichome branching. For example, when a gene called *TUBULIN FOLDING CO-FACTOR C* (*TFCC*) is affected, the normal organization of microtubules in mutant *tfcc* trichomes is disrupted and the resulting trichome has just two short branches, resembling the oar handles of a canoe. When yet another gene, *STICHEL*, is mutated, *sti* mutants don't develop any branches at all (**Figure c**). The underlying reason for this phenotype is not yet understood.

The examples described here underscore how complex molecular interactions affecting multiple aspects of a cell's functioning ultimately shape a cell's form and function. Because the genes that operate in trichomes are also involved in the development of other types of plant cells, understanding their effects and interactions promises to shed light on processes that operate to generate differentiated cells throughout the plant body.



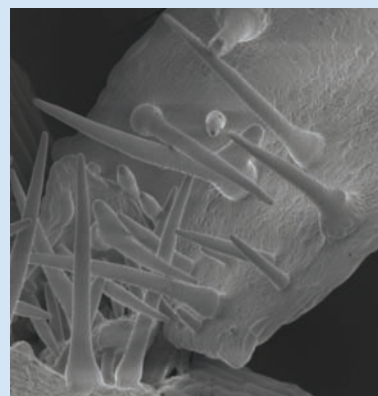
Jonathan Platt and Sharon Regan

**Figure a**  
Normal trichome from the epidermis of a leaf of *Arabidopsis thaliana*.



Daniel Szymanski, Plant Cell 10:2047

**Figure b**  
Five-pronged trichome from a *try* mutant.



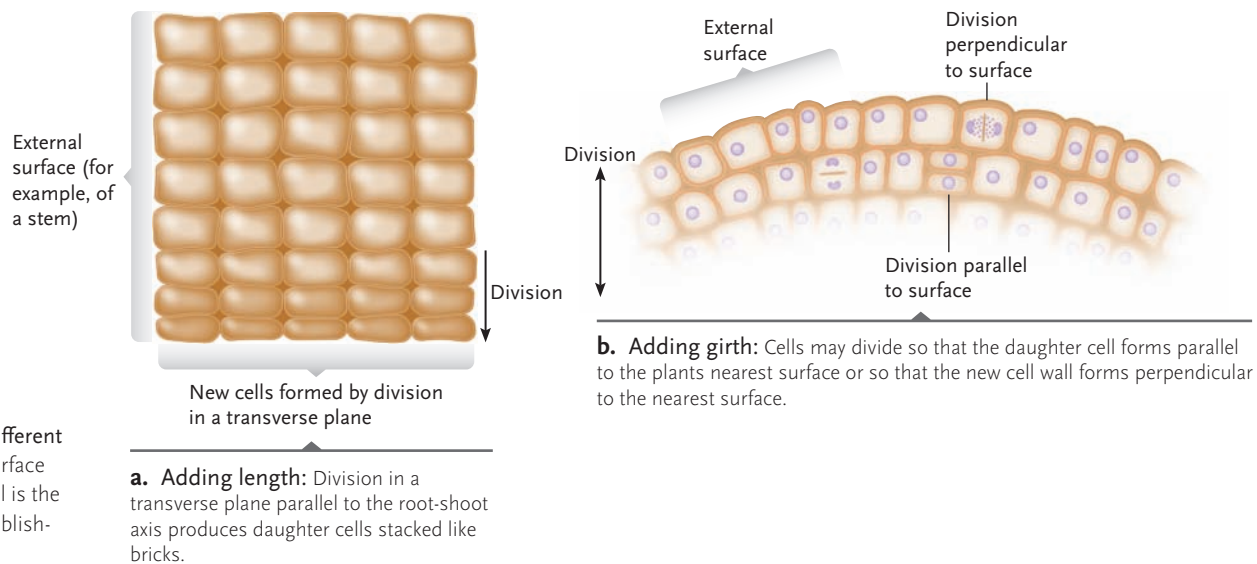
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**Figure c**  
The unbranched trichomes of an *sti* mutant.

chemical signals may cross from cortical to epidermal cells by way of plasmodesmata. When an epidermal cell receives signals from a single cortex cell, a series of genes are expressed in a cascade of effects that culminate in the expression of a gene called *GL2* (or *GLABRA2*). The product of *GL2* blocks the formation of root hairs. If, on the other hand, an epidermal cell aligns with two cortex cells, it receives signals from both and the cascade of gene effects blocks expression of *GL2*—and a root hair develops. *Insights from the Molecular Revolution* gives more examples of ways that trichomes such as root hairs have become popular experimental models for studying the differentiation of plant cells.

### Morphogenesis Shapes the Plant Body

As a plant embryo grows and tissues of differentiated cells form, the stage is set for different body regions to develop characteristic shapes and structures that correlate with their function. This process, called **morphogenesis**, shapes the new shoot and root parts produced by dividing cells in meristems. In animals, morphogenesis involves localized cell division and growth, as well as migration of cells and entire tissues from one site to another (see Chapter 48). Plant cells, however, are enclosed within thick walls and usually cannot move. Thus morphogenesis in plants relies on mechanisms that don't require mobility. One of these



**Figure 34.18**  
Plant cell division in different planes. The external surface nearest the dividing cell is the reference point for establishing division planes.

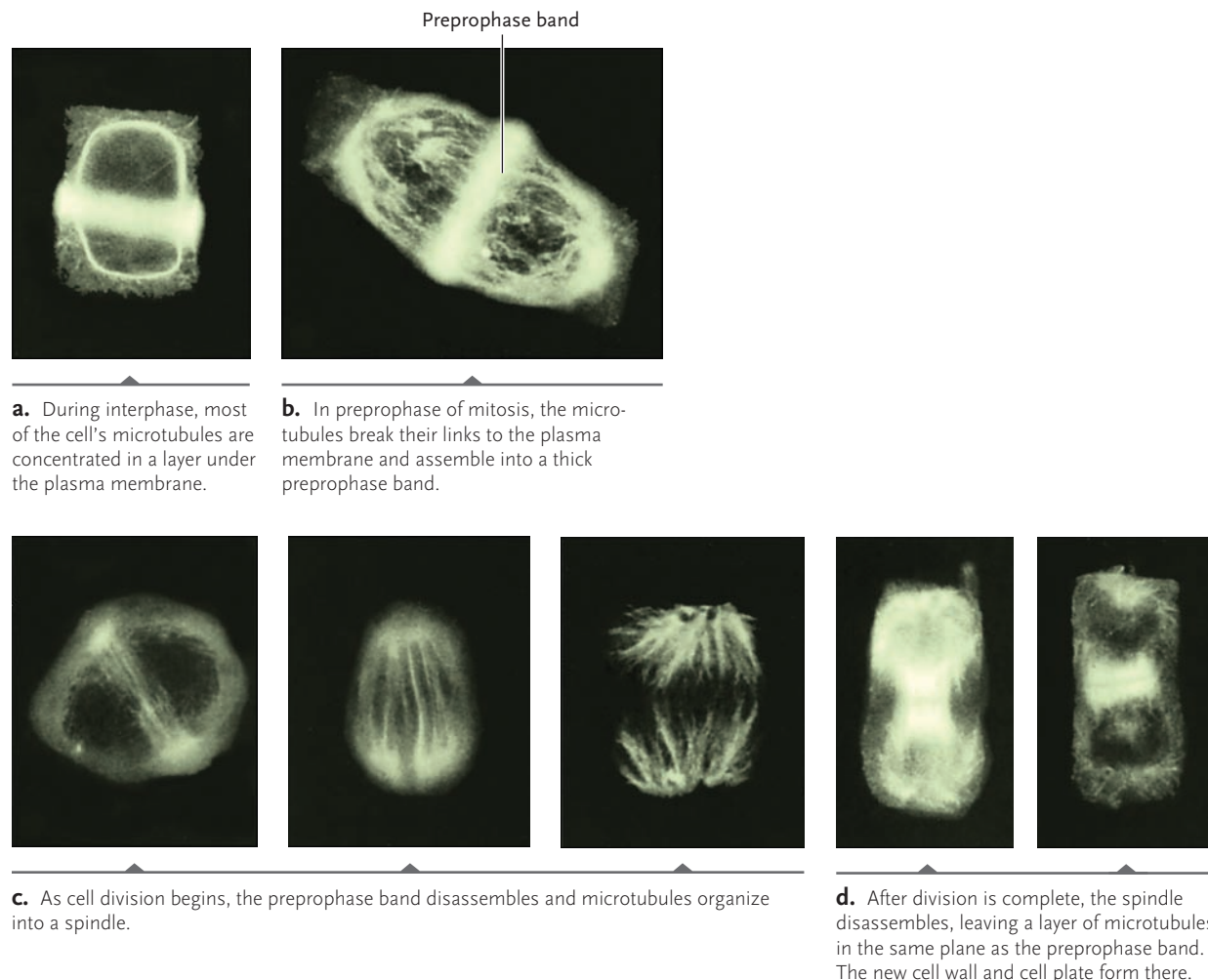
mechanisms is **oriented cell division**, which establishes the overall shape of a plant organ, and another is **cell expansion**, which enlarges the cells in specific directions in a developing organ.

**Oriented Cell Division.** As described in Chapter 31, roots and stems grow lengthwise as the division and

expansion of cells produce columns of cells parallel to the root–shoot axis. The cell divisions occur in a transverse plane—that is, new cell walls, and then the cell plate, form so that the cells become stacked one atop the other like wooden blocks (**Figure 34.18a**). A plant adds girth—increases in circumference—by way of cell divisions in other planes. For instance, new cell walls

**Figure 34.19**  
How the plane of cell division is determined in a plant cell. This series of micrographs shows events in onion (*Allium cepa*) root tip cells. The arrows mark the eventual location of the new cell wall.

(All: S. M. Wick, *J Cell Biol*, 89:685, 1987, Rockefeller University Press.)



may form parallel to the nearest plant surface, or perpendicular both to the nearest surface and to the transverse plane (Figure 34.18b).

You may recall from Chapter 10 that the cell plate forms during the cytokinesis phase of mitosis; it establishes the plane of the middle lamella that will eventually separate the parent and daughter cells. The capacity of dividing plant cells to synthesize a new cell plate in a different plane from the old one underlies morphogenesis in nearly all plant groups. In meristematic tissue, changes in the plane of cell division establish the direction in which structures such as lateral roots, branches, and leaf and flower buds will grow, and so gives the plant body its overall form.

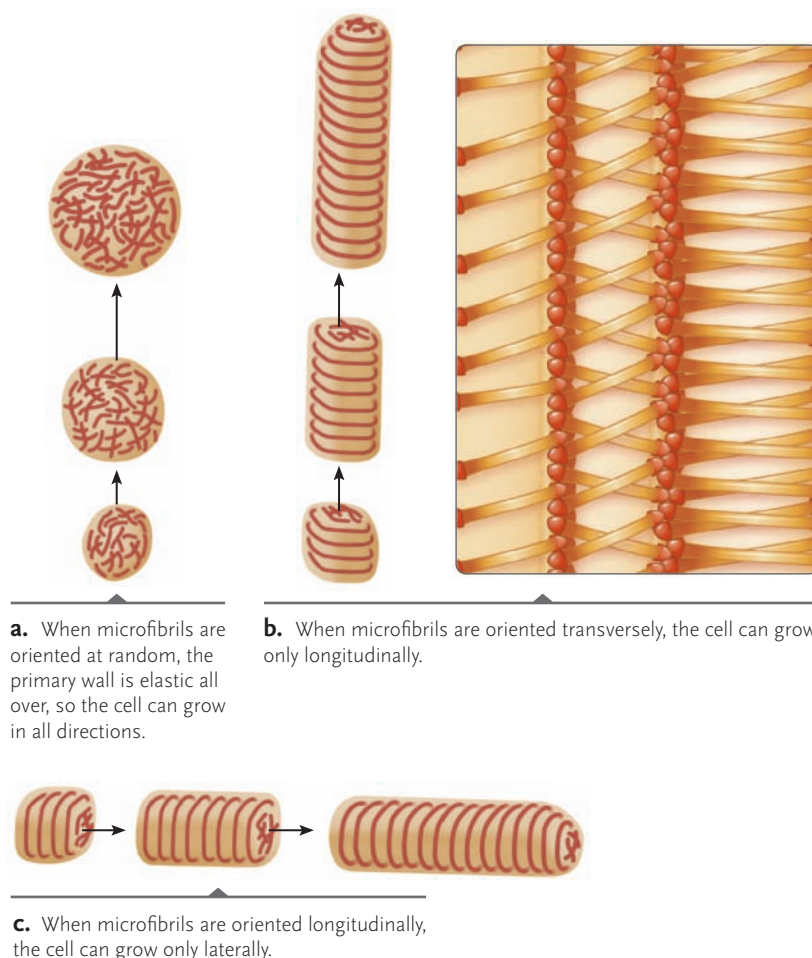
Figure 34.19 shows how the plane of a cell plate is established. While a plant cell destined to divide is still in interphase, hours before mitosis begins, the cell nucleus migrates to a particular location in the cell. The nucleus becomes surrounded by a layer of microtubules and microfilaments that radiate outward from it. Where the layer contacts the cell wall, a belt of microtubules and microfilaments called the *preprophase band* forms briefly, encircling the cell cytoplasm. The band usually disappears as mitosis gets underway in the cell, but its position marks the site where the cell plate forms during cytokinesis. Remnants of microfilaments may guide the edges of the developing cell plate into the proper position against the cell wall.

**Cell Expansion.** Once a cell has divided, the daughter cells expand to mature size. Yet plant cells are encased in a primary wall of nonliving material. Botanists are beginning to learn how the cell wall expands to accommodate the enlarging cell within.

Primary cell walls consist of a loose mesh of cellulose microfibrils embedded in a gel-like matrix. As plant cells mature, they may elongate to as much as 100 times their embryonic lengths. During this elongation, the cellulose meshwork is first loosened and then stretched. Turgor pressure supplies the force for stretching. The exact mechanism that loosens the wall structure is not known, although experiments indicate that it depends on a dramatic drop in pH. Some researchers suggest that an auxin in the cell cytoplasm may stimulate a plasma membrane proton pump that moves  $H^+$  into the cell wall (see Section 6.4). The acidic wall conditions may activate hydrolytic enzymes that break bonds between wall components, or they may promote loosening in some other way.

During expansion, enzyme complexes in the cell's plasma membrane synthesize new cellulose microfibrils from glucose in the cytoplasm. When each microfibril is fully formed, it is bound in place in the growing wall by pectins and other wall components.

The direction of cell expansion depends on the orientation of the newly formed cellulose microfibrils (Figure 34.20). If the microfibrils are randomly oriented,



**Figure 34.20**

**Cell expansion and the orientation of cellulose microfibrils.** In each cell, microtubules inherited from the parent cell are already oriented in prescribed patterns that govern how cellulose microfibrils will be oriented in the cell wall. Their orientation in turn governs the direction in which a cell can expand.

the cell expands equally in all directions. If they are oriented at right angles to the cell's long axis, the cell expands lengthwise. And if new fibrils are deposited parallel to the long axis of the cell, the cell expands laterally.

**Patterns of Cell Division during Early Growth.** Like the first mitotic division in an *Arabidopsis* zygote, it's not uncommon for cell divisions in a growing plant to be asymmetrical, so that one daughter cell ends up with more cytoplasm than the other. The unequal distribution of cytoplasm means that the daughter cells differ in their composition and structure, and the differences affect how they interact with their neighbors during growth, even though all cells carry the same genes. Their cytoplasmic differences and interactions with one another trigger selective gene expression. Such events seal the developmental fate of particular cell lineages. Their descendant cells divide in prescribed planes and expand in set directions, producing plant parts with diverse shapes and functions.

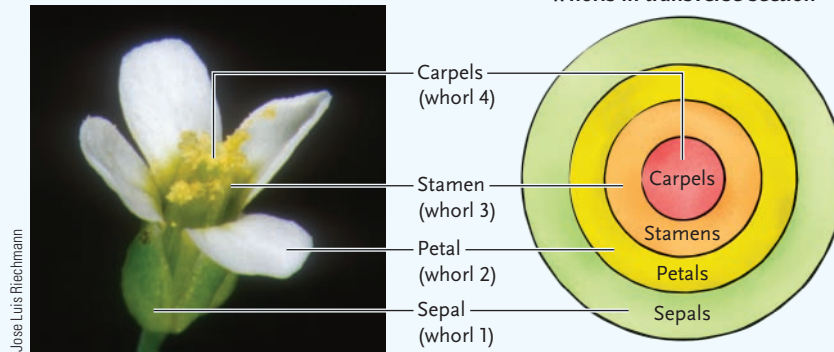
## Figure 34.21 Experimental Research

### Probing the Roles of Floral Organ Identity Genes

**QUESTION:** What are the genetic mechanisms that govern the formation of the parts of a flower?

**EXPERIMENTS:** Meyerowitz and his colleagues grew *Arabidopsis thaliana* plants having mutated, inactivated versions of the genes suspected of controlling the proper development of floral organs. They compared the types and arrangements of floral organs in the test plants with the organs present in normal, wild-type *A. thaliana* flowers.

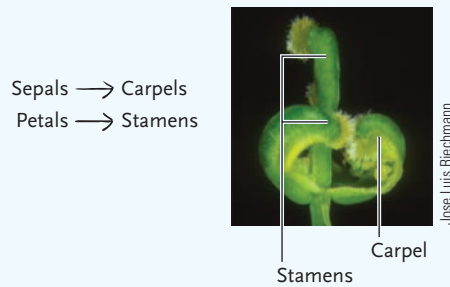
**a. Normal *A. thaliana***



**Normal arrangement of organs:**  
carpels in whorl 4, stamens in whorl 3,  
petals in whorl 2, and sepals in whorl 1

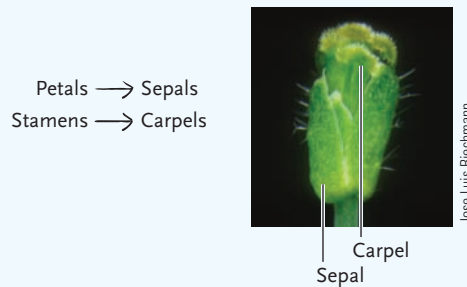
**RESULTS:** At least three classes of homeotic genes (A, B, and C) regulate different aspects of normal floral organ development.

**b. When mutation inactivates the *APETALA2* gene, class A genes are not expressed.**



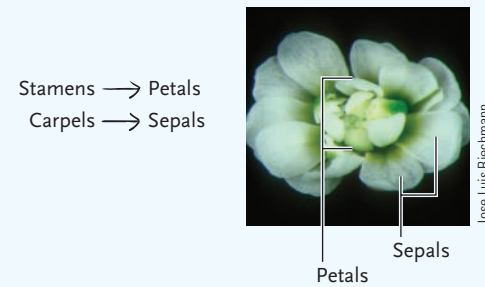
Stamens replace petals and carpels replace sepals. Organ identity in the other whorls does not change.

**c. When mutation inactivates the *APETALA3* or *PISTILLATA* gene, class B genes are not expressed.**



Carpels replace stamens and sepals replace petals. Organ identity in the other whorls does not change.

**d. When mutation inactivates the *AGAMOUS* gene, class C genes are not expressed.**



No carpels; instead petals develop in whorl 3 and a version of a floral meristem develops where whorl 4 would normally be. It gives rise to extra petals and sepals. Organ identity in other whorls does not change.

Further experiments with double mutants (inactivation of both A and B, A and C, and B and C) all produce abnormal flowers. For example, only carpels develop in mutants having only an active C class gene, and only sepals develop in plants having only an active B class gene.

**e. Overlapping activity fields of floral organ identity genes**

<b>Carpels</b>			<b>C</b>	<b>E</b>	<b>Whorl 4</b>
<b>Stamens</b>		<b>B</b>	<b>C</b>	<b>E</b>	<b>Whorl 3</b>
<b>Petals</b>	<b>A</b>	<b>B</b>		<b>E</b>	<b>Whorl 2</b>
<b>Sepals</b>	<b>A</b>				<b>Whorl 1</b>

**CONCLUSIONS:** In *A. thaliana*, A, B, and C activity genes, expressed alone or in pairs, underlie the development of a normal pattern of floral organs. The fields of activity overlap. In addition, A and C activity apparently counteract each other, and if one is absent the other can spread beyond the whorls where it normally appears. Subsequent research revealed that a fourth E class of gene activity is required for proper expression of other organ identity genes.

## Regulatory Genes Guide the Development of Floral Organs

Research with several plant species has shed light on the genetic mechanisms that govern the formation of the parts of a flower. For example, experiments with *Arabidopsis* carried out by Elliot Meyerowitz and his colleagues at the California Institute of Technology showed that *floral organ homeotic genes* regulate the development of the sepals, petals, stamens, and carpels in flowers.

The Meyerowitz team studied plants with various mutations in floral organs. By observing the effects of specific mutations on the structure of *Arabidopsis* flowers, the investigators eventually identified three classes of homeotic gene activity—which they named A, B, and C—that regulate different aspects of normal flower development. Subsequent studies by other scientists identified an E class of gene activity that appears to be an essential partner in the functioning of A, B, and C class genes. The effects of the genes overlap, so that A, B, and C class genes are expressed in two whorls, and E class genes in three: Class A genes are expressed in whorls 1 and 2 (sepals and petals), class B genes in whorls 2 and 3 (petals and stamens), class C genes in whorls 3 and 4 (stamens and carpels), and class E genes in whorls 2, 3, and 4 (Figure 34.21).

Abnormal floral patterns such as those in Figure 34.21b–d show how mutations in the floral organ homeotic genes can affect the identity of flower parts. For example, a mutation that deactivates the A-class gene *APETALA2* produces a flower with carpels and stamens in whorl 1 (see Figure 34.21b). Another intriguing finding is that the A and C activity classes normally oppose each other. When no A gene is expressed, C activity spreads into whorls where the A usually occurs, and vice versa. Subsequent studies have examined many other floral homeotic genes, as well as the genes that control the various gene classes.

As the genes governing flower development are isolated, they can be cloned and their nucleotide se-

quences defined and manipulated. Such cloned genes already are of keen interest in plant genetic engineering, because food grains such as wheat and many other vital agricultural commodities come directly or indirectly from flowers.

## Leaves Arise from Leaf Primordia in a Closely Regulated Sequence

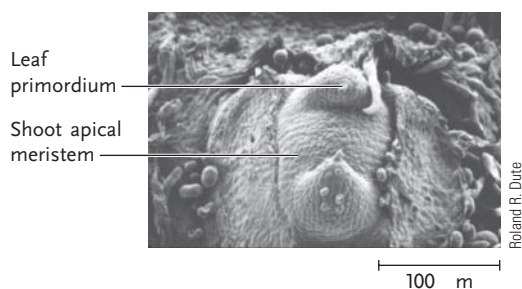
A mature leaf may have many millions of differentiated cells organized into tissues such as epidermis and mesophyll. As described in Chapter 31, leaves develop from leaf primordia that arise just behind the tips of shoot apical meristems (Figure 34.22).

**Clonal analysis** has opened a window on many aspects of plant development, including how leaf primordia originate and give rise to leaves. In this method, the investigator cultures meristematic tissue that contains a mutated embryonic cell having a readily observable trait, such as the absence of normal pigment. (In the laboratory, this kind of mutation can be induced by chemicals or radiation.) The unusual trait then serves as a marker that identifies the mutant cell's clonal descendants, making it possible to map the growing structure. Researchers have used clonal analysis to study leaf development in garden peas, tomatoes, grasses, and tobacco, among others.

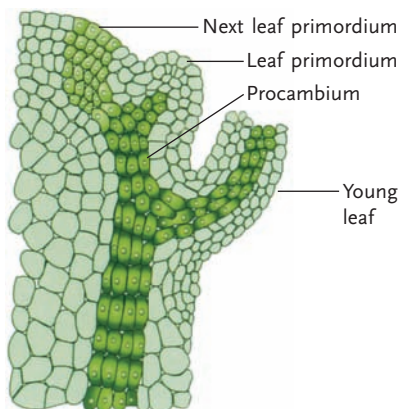
Like flowers, leaves arise through a developmental program that begins with gene-regulated activity in meristematic tissue. Hormones or other signals may arrive at target cells via the stem's vascular tissue, activating genes that regulate development. Studies show that small phloem vessels first penetrate a young leaf primordium almost immediately after it begins to bulge out from the underlying meristematic tissue, and xylem soon follows. The early phloem connections are especially vital to the leaf's survival, because the leaf does not begin photosynthesis until it attains one-third of its mature size.

A growing primordium becomes cone-shaped, wider at its base than at its tip. At a certain point, mitosis speeds up in cells along the flanks of the lengthening

a. Leaf primordia of *Coleus*



b. Early stages of leaf development



**Figure 34.22**

Early stages in leaf development. (a) Leaf primordia at the shoot tip of *Coleus*, a genus that includes several popular house plants. (b) Diagram showing leaf primordia in different stages of development. See also Figure 34.12a, which shows the progression of leaves that form during the early growth and development of a eudicot.

cone. In eudicots, the rapid cell divisions occur perpendicular to the surface and produce the leaf blade. In monocot grasses, which have long, narrow leaves, vertical “files” of cells develop as cells in the meristem at the base of the cone divide in a plane parallel to the surface. The ultimate shape of a leaf depends in part on variations in the plane and rate of these cell divisions.

Cells at the leaf tip, and those of xylem and phloem that service it, are the oldest in the leaf, and it is here that photosynthesis begins. Commonly, leaf tip cells also are the first to stop dividing. By the time a leaf has expanded to its mature size, all mitosis has ended and the leaf is a fully functional photosynthetic organ.

In nature, genes that govern leaf and flower development switch on or off in response to changing environmental conditions. Their signals determine the course of a plant’s vegetative growth throughout its life. In many perennials, new leaves begin to develop inside buds in autumn, then become dormant until the following spring, when external conditions favor further growth. Environmental cues stimulate the gene-

guided production of hormones that travel through the plant in xylem and phloem, triggering renewed leaf growth and expansion. Leaves and other shoot parts also age, wither, and fall away from the plant as hormonal signals change. The far-reaching effects of plant hormones on growth and development are the subject of Chapter 35.

## STUDY BREAK

1. What is a homeotic gene? Give at least two examples of plant tissues such genes might govern in a species such as *Arabidopsis*.
2. What are the two basic mechanisms of morphogenesis in plants? Describe the patterns of cell division by which a plant part (a) grows longer and (b) adds girth.
3. Summarize the gene-guided developmental program that gives rise to a leaf.

## UNANSWERED QUESTIONS

### What are the signaling events that mediate pollen-tube guidance during compatible pollination?

As you learned in this chapter, after pollen lands on the surface of the carpel, it forms a pollen tube, which then invades the carpel, migrates past several different cell types, and enters the micropyle to fertilize an egg and central cell. Recent work has shown that pollen-tube migration is mediated by a series of cell–cell interactions such as attraction, repulsion, and adhesion. However, most of these conclusions have been based on analyzing static images and fixed tissues, and it has been hypothesized that many more subtle, dynamic interactions between the pollen tube and female cells exist to ensure compatible pollination. It has been shown, for example, that pollen tubes gain the competence to successfully find the ovules only when they grow on the pistil tissues, a process that is functionally analogous to the transformation that mammalian spermatozoa undergo after residence for a finite amount of time in the female reproductive tract. It was also recently demonstrated that once a pollen tube penetrates the ovule, additional pollen tubes are prevented from gaining access into the targeted ovule, a process that is functionally analogous to the prevention of polyspermy by a fertilized mammalian egg. These novel signaling events are spurring researchers to take a closer look at pollen-tube guidance to ovules. Only when such signaling events are described can appropriate efforts be taken to identify the cues that mediate these events (see next question).

What kinds of approaches are being taken to identify novel signaling events? Researchers usually first identify a mutant plant that is defective in any of the pollen-tube guidance steps that are essential for successful fertilization. Subsequently, they analyze the defects to learn more about how this process normally happens. Other researchers develop microscopy-based real-time assays to directly observe pollen-tube behavior with a variety of female tissues.

### What are the chemical cues from female tissues that facilitate compatible pollination?

As you learned in this chapter, if a pollen tube lands on a compatible stigma, chemical cues produced by the female tissue then guide the pollen tube from the stigma to the embryo sac of an ovule. Recent research has revealed that cues produced by both sporophyte and gametophyte are essential for proper guidance of pollen tubes to ovules. Despite these advances, the identities of these cues remain unknown. What are the hurdles that have hampered efforts to uncover pollen-tube navigation cues of even known signaling events described above? First, the pistil tissue within which the pollen tube elongates to the ovule is comprised of several types of tissue, including stigma, style, and transmitting tract, and these tissues are not readily accessible. Second, analyzing the dynamic responses of pollen tubes is difficult given that pollen-tube navigation occurs well within opaque pistils. Third, it appears that multiple, stage-specific, short-range, and readily labile signals produced in minute quantities mediate pollen-tube guidance. However, recent development of global approaches that are highly sensitive and assays that directly monitor pollen-tube elongation offer hope that guidance cues will be uncovered sooner rather than later.



Ravi Palanivelu is an assistant professor in the Department of Plant Sciences at the University of Arizona. His current research focuses on the isolation and characterization of pollen-tube guidance signals during *Arabidopsis* reproduction, with the long-term goal of understanding the molecular basis of how cells communicate with each other. To learn more about Dr. Palanivelu’s research, go to <http://www.ag.arizona.edu/research/ravilab>.



## Review

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### 34.1 Overview of Flowering Plant Reproduction

- In most flowering plant life cycles, a multicellular diploid sporophyte (spore-producing plant) stage alternates with a multicellular haploid gametophyte (gamete-producing plant) stage. The sporophyte develops roots, stems, leaves, and, at some point, flowers. The separation of a life cycle into diploid and haploid stages is called alternation of generations (Figure 34.2).

**Animation: Flowering plant life cycle**

### 34.2 The Formation of Flowers and Gametes

- A flower develops at the tip of a floral shoot. It can have up to four whorls supported by the receptacle. The calyx and corolla consist of the sepals and petals, respectively. The third whorl consists of stamens, and carpels make up the innermost whorl (Figure 34.3).
- The anther of a stamen contains sacs where pollen grains develop. If compatible pollen lands on the carpel's stigma, which contains an ovary in which eggs develop, fertilization takes place.
- A complete flower has both male and female reproductive parts. In monoecious species each plant has both types of flowers; in dioecious species the “male” and “female” flowers are on different plants (Figure 34.4).
- In pollen sacs, meiosis produces haploid microspores. Mitosis inside each microspore produces a pollen grain, an immature male gametophyte. One of its cells develops into two sperm cells, the male gametes of flowering plants. Another cell produces the pollen tube (Figures 34.5 and 34.6).
- An ovule forms inside a carpel, on the wall of the ovary. Development in the ovule produces a female gametophyte—the embryo sac with egg cell.
- In the ovule, meiosis produces four haploid megaspores. Usually all but one disintegrate. The remaining megaspore undergoes mitosis three times without cytokinesis, producing eight nuclei in a single large cell. Two of these (polar nuclei) migrate to the center of the cell. When cytokinesis occurs, cell walls form around the nuclei, with the two polar nuclei enclosed in a single wall. The result is the seven-celled embryo sac, one cell of which is the haploid egg. The cell containing polar nuclei will help give rise to endosperm.

**Animation: Floral structure and function**

**Animation: Flower parts**

**Animation: Microspores to pollen**

**Animation: Apple fruit structure**

### 34.3 Pollination, Fertilization, and Germination

- Upon pollination, the pollen grain resumes growth. A pollen tube develops, and mitosis of the male gametophyte's sperm-producing cell produces two sperm nuclei (Figure 34.7).
- In double fertilization, one sperm nucleus fuses with one egg nucleus to form a diploid ( $2n$ ) zygote. The other sperm nucleus and the two polar nuclei of the remaining cell also fuse, forming

a cell that will give rise to triploid ( $3n$ ) endosperm in the seed (Figure 34.8).

- After the endosperm forms, the ovule expands, and the embryonic sporophyte develops. A mature ovule is a seed. Inside the seed, the embryo has a lengthwise axis with a root apical meristem at one end and a shoot apical meristem at the other.
- Eudicot embryos have two cotyledons. The embryonic shoot consists of an upper epicotyl and a lower hypocotyl; also present is an embryonic root, the radicle. The single cotyledon of a monocot forms a scutellum that absorbs nutrients from endosperm. Apical meristems of a monocot embryo are protected by a coleoptile over the shoot tip and a coleorhiza over the radicle (Figure 34.9).
- A fruit is a matured or ripened ovary. Fruits protect seeds and disperse them by animals, wind, or water.
- Fruits are simple, aggregate, or multiple, depending on the number of flowers or ovaries from which they develop. Fruits also vary in the characteristics of their pericarp, which surrounds the seed (Figure 34.10).
- The seeds of most plants remain dormant until external conditions such as moisture, temperature, and day length favor the survival of the embryo and the development of a new sporophyte (Figures 34.11–34.13).

**Animation: Bee-attracting flower pattern**

### 34.4 Asexual Reproduction of Flowering Plants

- Many flowering plants also reproduce asexually, as when new plants arise by mitosis at nodes or buds along modified stems of the parent plant. New plants also may arise by vegetative propagation (Figure 34.14).
- Tissue culture methods for developing new plants from a parent plant's somatic (nonreproductive) cells include somatic embryogenesis and protoplast fusion (Figure 34.15).

**Animation: Eudicot life cycle**

**Animation: Eudicot seed development**

### 34.5 Early Development of Plant Form and Function

- In plants that reproduce sexually, development starts at fertilization. Early on, a new embryo acquires its root–shoot axis, and cells in different regions begin to become specialized for particular functions (Figure 34.16). In morphogenesis, body regions develop characteristic shapes and structures that correlate with their function (Figure 34.17).
- Dividing plant cells can synthesize a new cell plate in a different plane from the old one. Such changes establish the direction in which structures such as lateral roots, branches, and leaf and flower buds grow (Figures 34.18 and 34.19).
- Chemical signals that help guide morphogenesis appear to act on certain cells in meristematic tissue, activating homeotic genes that ultimately regulate cell division and differentiation (Figures 34.20 and 34.21).

**Animation: ABC model for flowering**

## Questions

### Self-Test Questions

- An angiosperm life cycle includes:
  - meiosis within the male gametophyte to produce sperm.
  - meiosis within the female gametophyte to produce eggs.
  - meiosis within the ovary to produce megaspores.
  - fertilization to produce microspores.
  - fertilization to produce megaspores.
- In a flower:
  - the ovary contains the ovule.
  - the stamens support the petals.
  - the anther contains the megaspores.
  - the carpel includes the sepals.
  - the corolla includes the receptacle.
- Double fertilization in a flower means:
  - six sperm fertilize two groups of three eggs each.
  - one sperm fertilizes the egg; a second sperm fertilizes the  $2n$  mother cell.
  - one microspore becomes a pollen grain; the other microspore becomes a sperm-producing cell.
  - one pollen grain can make sperm nuclei and a pollen tube.
  - one sperm can fertilize two endosperm mother cells.
- A seed is best described as a (an):
  - epicotyl.
  - endosperm.
  - ovary.
  - mature spore.
  - mature ovule.
- The primary root develops from the embryonic:
  - epicotyl.
  - hypocotyl.
  - coleoptile.
  - radicle.
  - plumule.
- Which of the following is *not* a step in the germination of a monocot seed?
  - Enzymes secreted into the endosperm digest the endosperm cell wall and macromolecules.
  - The embryo imbibes water and then produces gibberellin.
  - The embryo absorbs nutrients released from the endosperm.
  - Endosperm develops as a food reserve.
  - Gibberellin acts on the cells of the aleurone and scutellum to encode hydrolytic enzymes.
- A student cuts off a leaflet from a plant and places it in a glass of water. Within a week roots appear on the base of the cutting. A month later she places the growing cutting into soil and it grows to the full size of the “parent” plant. This is an example of:
  - parthenocarpy.
  - fragmentation.
  - grafting.
  - vegetative reproduction.
  - tissue culture propagation.
- Which of the following is *not* an example of pattern formation in developing plants?
  - an epidermal cell receiving developmental signals from a cortical cell
  - the loosening of the cell wall to allow the elongation of selected cells to reach mature size
  - regulation by homeotic genes of the position of different flower parts
  - oriented cell division that establishes the shape of an organ
  - cell expansion that directs specific cells to undergo mitosis at a given time and place
- During the development of a leaf:
  - mitotic cell divisions occur on planes specific to different plant groups.
  - xylem vessels are the first to penetrate the leaf primordium.
  - the growing leaf primordium becomes wider at its base than at its tip.

- the leaf primordium bulges from the region behind the shoot apical meristem.
  - All of the above occur during leaf development.
- In spring a lone walnut tree in your backyard develops attractive white flowers, and by the end of summer roughly half the flowers have given rise to the shelled fruits we know as walnuts. Walnut trees are self-pollinating. Assuming that pollination was 100% efficient in the case of your tree, which of the following statements best describes your tree’s reproductive parts?
    - Its flowers are in the botanical category of “perfect” flowers.
    - The tree is monoecious.
    - The tree is dioecious.
    - The tree has imperfect, monoecious flowers.
    - a and b together provide the best description of the tree’s flowers.

### Questions for Discussion

- A plant physiologist has succeeded in cloning a gene for pest resistance into petunia cells. How can she use tissue culture to propagate a large number of petunia plants having the gene?
- A large tree may have tens of thousands of shoot tips, and the cells in each tip can differ genetically from cells in other tips, sometimes substantially. Propose a hypothesis to explain this finding, and speculate about how it might be beneficial to the plant. How might this sort of natural variation be useful to human society?
- Grocery stores separate displays of fruits and vegetables according to typical uses for these plant foods. For instance, bell peppers, cucumbers, tomatoes, and eggplants are in the vegetable section, while apples, pears, and peaches are displayed with other fruits. How does this practice relate to the biological definition of a fruit?

### Experimental Analysis

The developmental genetics of flowers are of keen interest in plant biotechnology, especially with regard to food plants such as wheat and rice. Outline a research program for a crop species that would exploit the genetics of flower development, including the effects of homeotic genes, to engineer a more productive variety.

### Evolution Link

Botanists estimate that half or more of angiosperm species may be polyploids that arose initially through hybridization. *Polyploidy*—having more than a diploid set of the parental chromosomes—can result from nondisjunction of homologous chromosomes during meiosis, or when cytokinesis fails to occur in a dividing cell. *Hybridization* is the successful mating of individuals from two different species. Such an interspecific hybrid is likely to be sterile because it has uneven numbers of parental chromosomes, or because the chromosomes are too different to pair during meiosis. A sterile hybrid may reproduce asexually, however, and if by chance its offspring should become polyploid, that plant will be fertile because the original set of chromosomes will have homologs that can pair normally during meiosis. Explain why both the hybrid parent and fertile polyploid offspring may be considered a new species, and describe at least two ways in which this route to speciation differs from speciation in the animal kingdom.

### How Would You Vote?

Microencapsulated pesticides are easy to apply and effective for long periods. But they are about the size of pollen grains and are a tempting but toxic threat to certain pollinators. Should we restrict their use? Go to [www.thomsonedu.com/login](http://www.thomsonedu.com/login) to investigate both sides of the issue and then vote online.