

# 38

## Angiosperm Reproduction and Biotechnology



▲ **Figure 38.1** Why is this wasp trying to mate with this flower?

### KEY CONCEPTS

- 38.1 Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle**
- 38.2 Flowering plants reproduce sexually, asexually, or both**
- 38.3 Humans modify crops by breeding and genetic engineering**

### OVERVIEW

#### Flowers of Deceit

Male wasps of the species *Campsoscolia ciliata* often attempt to copulate with the flowers of the Mediterranean orchid *Ophrys speculum* (Figure 38.1). During this encounter, a sac of pollen becomes glued to the insect's body. Eventually frustrated, the wasp flies off and deposits the pollen onto another *Ophrys* flower that has become the object of his misplaced ardor. *Ophrys* flowers offer no reward such as nectar to the male wasps, only sexual frustration. So what makes the

male wasps so enamored of this orchid? The traditional answer has been that the shape of the orchid's largest petal and the frill of orange bristles around it vaguely resemble the female wasp. These visual cues, however, are only part of the deception: *Ophrys* orchids also emit chemicals with a scent similar to that produced by sexually receptive female wasps.

This orchid and its wasp pollinators are one example of the amazing ways in which angiosperms (flowering plants) reproduce sexually with spatially distant members of their own species. Sex, however, is not their only means of reproduction. Many species also reproduce asexually, creating offspring that are genetically identical to the parent.

An unusual aspect of the orchid and wasp example is that the insect does not profit from interacting with the flower. In fact, by wasting time and energy, the wasp is probably rendered less fit. More typically, a plant lures an animal pollinator to its flowers not with offers of sex but with rewards of energy-rich nectar or pollen. Thus, both plant and pollinator benefit; that is, the relationship is mutually beneficial. Participating in such beneficial relationships with other organisms is very common in the plant kingdom. In fact, in recent evolutionary times, some flowering plants have formed relationships with an animal that not only disperses their seeds but also provides the plants with water and mineral nutrients and vigorously protects them from encroaching competitors, pathogens, and predators. In return for these favors, the animal typically gets to eat a fraction of the plants' seeds and fruits. The plants involved in these reciprocally beneficial interactions are called crops; the animals are humans.

Since the origins of crop domestication over 10,000 years ago, plant breeders have genetically manipulated the traits of a few hundred wild angiosperm species by artificial selection, transforming them into the crops we grow today. Genetic engineering has dramatically increased the variety of ways and the speed with which we can now modify plants.

In Chapters 29 and 30, we approached plant reproduction from an evolutionary perspective, tracing the descent of land plants from algal ancestors. Here, we'll explore the reproductive biology of flowering plants in greater detail because they are the most important group of plants in most terrestrial ecosystems and in agriculture. After discussing the sexual and asexual reproduction of angiosperms, we'll examine the role of humans in genetically altering crop species, as well as the controversies surrounding modern plant biotechnology.

### CONCEPT 38.1

#### Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle

The life cycles of plants are characterized by an alternation of generations, in which multicellular haploid ( $n$ ) and diploid ( $2n$ )

generations take turns producing each other (see Figures 29.5 and 30.10). The diploid plant, the sporophyte, produces haploid spores by meiosis. These spores divide by mitosis, giving rise to the multicellular gametophytes, the male and female haploid plants that produce gametes (sperm and eggs). **Fertilization**, the fusion of gametes, results in diploid zygotes, which divide by mitosis and form new sporophytes. In angiosperms, the sporophyte is the dominant generation: It is larger, more conspicuous, and longer-lived than the gametophyte. Over the course of seed plant evolution, gametophytes became reduced in size and wholly dependent on the sporophyte for nutrients. Angiosperm gametophytes are the most reduced of all plants, consisting of only a few cells. **Figure 38.2** reviews the angiosperm life cycle, which is shown in more detail in Figure 30.10. The key derived traits of the angiosperm life cycle can be remembered as the “three Fs”—flowers, double fertilization, and fruits. Since angiosperms, along with gymnosperms, are seed plants, a knowledge of seed structure and function is also critical to understanding the angiosperm life cycle.

### Flower Structure and Function

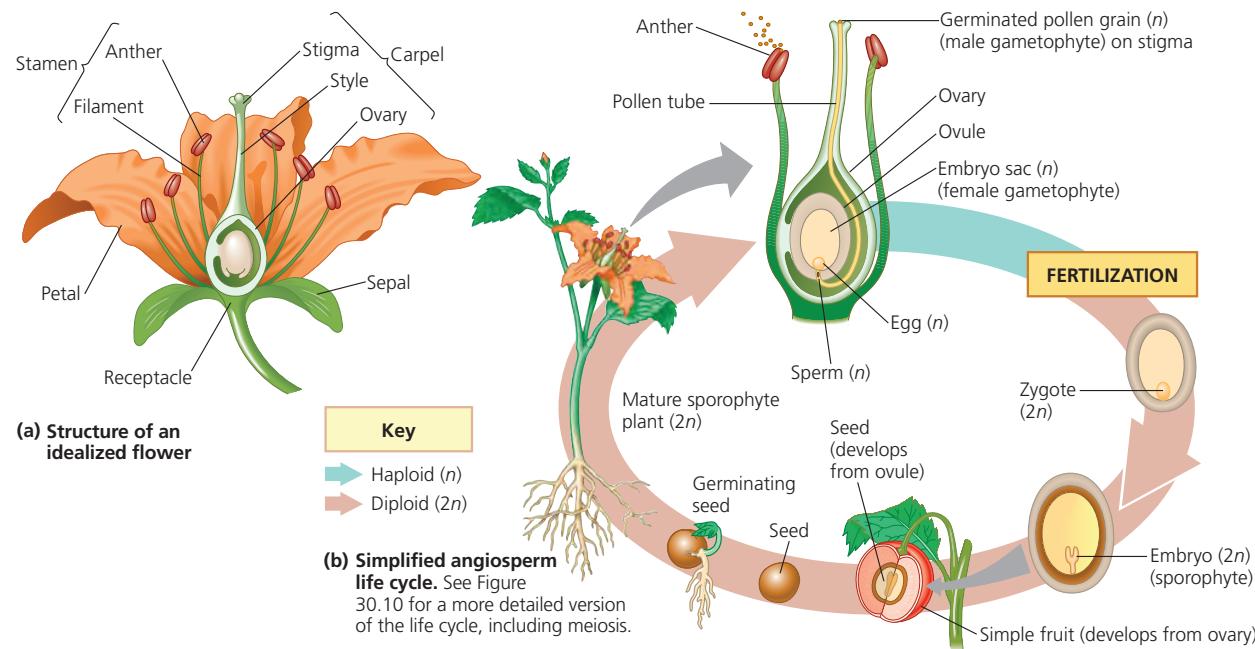
Flowers, the reproductive shoots of angiosperm sporophytes, are typically composed of four whorls of modified leaves called floral organs. Unlike vegetative shoots, flowers are determinate shoots; they cease growing after the flower and fruit are formed.

Floral organs—**sepals**, **petals**, **stamens**, and **carpels**—are attached to a part of the stem called the **receptacle**. Stamens and carpels are reproductive organs, whereas sepals and petals

are sterile. Sepals, which enclose and protect unopened floral buds, are usually more leafy in appearance than the other floral organs. Petals are typically more brightly colored than sepals and advertise the flower to insects and other pollinators.

A stamen consists of a stalk called the **filament** and a terminal structure called the **anther**; within the anther are chambers called microsporangia (pollen sacs) that produce pollen. A carpel has an **ovary** at its base and a long, slender neck called the **style**. At the top of the style is a generally sticky structure called the **stigma** that captures pollen. Within the ovary are one or more **ovules**; the number of ovules depends on the species. The flower shown in Figure 38.2 has a single carpel, but many species have multiple carpels. In most species, two or more carpels are fused into a single structure; the result is an ovary with two or more chambers, each containing one or more ovules. The term **pistil** is sometimes used to refer to a single carpel or two or more fused carpels.

**Complete flowers** have all four basic floral organs (see Figure 38.2a). Some species have **incomplete flowers**, lacking sepals, petals, stamens, or carpels. For example, most grass flowers lack petals. Some incomplete flowers are sterile, lacking functional stamens and carpels; others are *unisexual*, lacking either stamens or carpels. Flowers also vary in size, shape, color, odor, organ arrangement, and time of opening. Some are borne singly, while others are arranged in showy clusters called **inflorescences**. For example, a sunflower’s central disk consists of hundreds of tiny incomplete flowers, and what look like petals are actually sterile flowers (see Figure 1.3). Much of floral diversity represents adaptation to specific pollinators.



▲ **Figure 38.2** An overview of angiosperm reproduction.

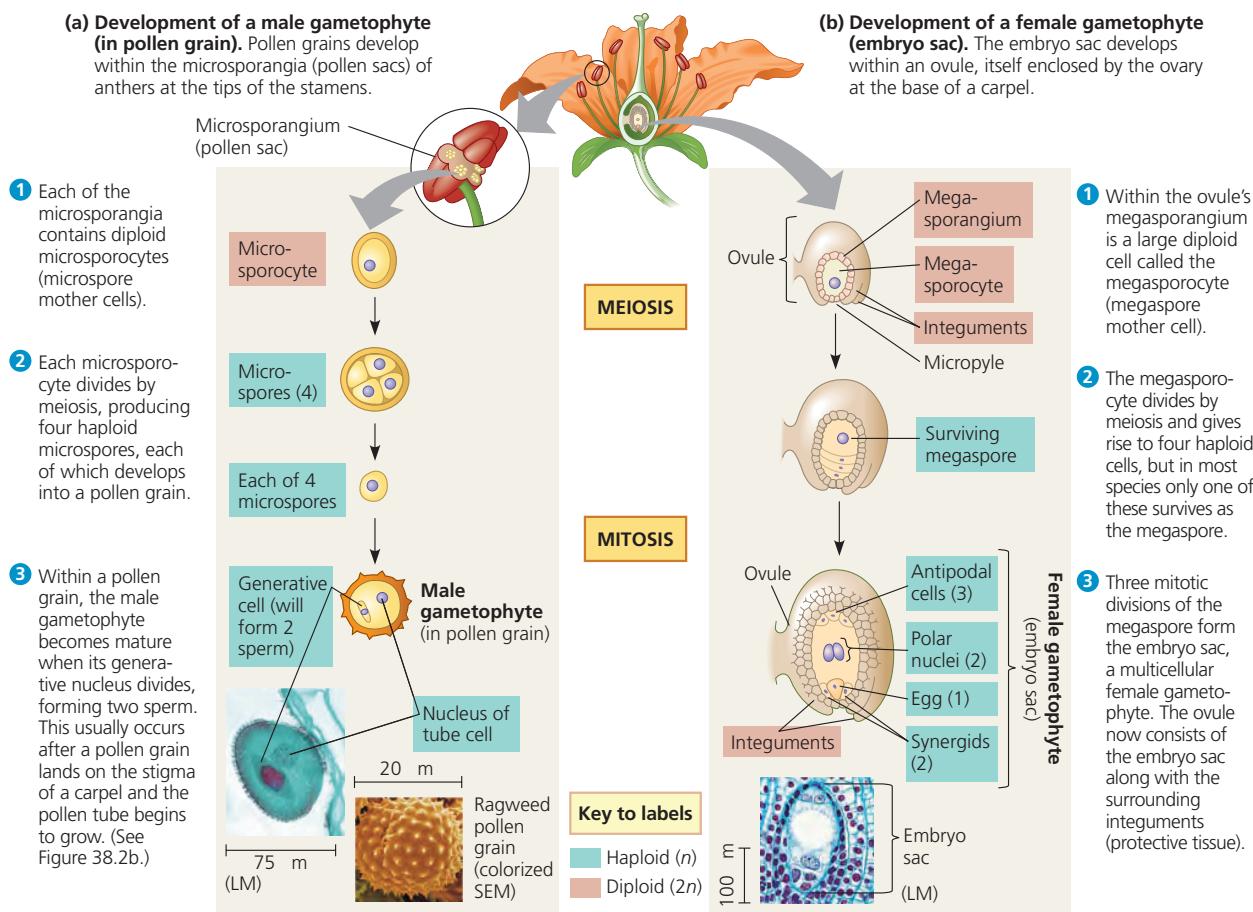
### Development of Male Gametophytes in Pollen Grains

Each anther contains four microsporangia, also known as pollen sacs. Within the microsporangia are many diploid cells called *microsporocytes*, or microspore mother cells (**Figure 38.3a**). Each microsporocyte undergoes meiosis, forming four haploid **microspores**, each of which eventually gives rise to a haploid male gametophyte. Each microspore then undergoes mitosis, producing a male gametophyte consisting of only two cells: the *generative cell* and the *tube cell*. Together, these two cells and the spore wall constitute a **pollen grain**. The spore wall, which consists of material produced by both the microspore and the anther, usually exhibits an elaborate pattern unique to the species. During maturation of the male gametophyte, the generative cell passes into the tube cell, and the spore wall is completed. The tube cell now has a completely free-standing cell inside it. After the microsporangium breaks open and releases the pollen, a pollen grain may be transferred to a receptive surface of a stigma. There, the tube cell produces the **pollen tube**, a long cellular protuberance that delivers sperm to the female gametophyte. Pollen tubes

can grow very quickly, at rates of 1 cm/hr or more. As a pollen tube elongates through the style, the generative cell usually divides and produces two sperm cells, which remain inside the tube cell (see Figure 30.10). The pollen tube grows through the style and into the ovary, where it releases the sperm cells in the vicinity of the female gametophyte.

### Development of Female Gametophytes (Embryo Sacs)

Among angiosperm species, there are over 15 variations in the development of the female gametophyte, also known as an **embryo sac**. We'll focus on just one common variation. The entire process occurs in a tissue within each ovule called the megasporangium. Two *integuments* (layers of protective sporophytic tissue that will develop into the seed coat) surround each megasporangium except at a gap called the *micropyle*. Female gametophyte development begins when one cell in the megasporangium of each ovule, the *megasporocyte* (or megasporocyte mother cell), enlarges and undergoes meiosis, producing four haploid **megaspores** (**Figure 38.3b**). Only one megasporite survives; the others degenerate.



▲ **Figure 38.3** The development of male and female gametophytes in angiosperms.

The nucleus of the surviving megasporangium divides by mitosis three times without cytokinesis, resulting in one large cell with eight haploid nuclei. The multinucleate mass is partitioned by membranes into a multicellular female gametophyte—the embryo sac. The cell fates of the nuclei are determined by a gradient of the hormone auxin originating near the micropyle. At the micropylar end, two cells called synergids

flank the egg and help attract and guide the pollen tube to the embryo sac. At the opposite end of the embryo sac are three antipodal cells of unknown function. The other two nuclei, called polar nuclei, are not partitioned into separate cells but share the cytoplasm of the large central cell of the embryo sac. The ovule, which will become a seed, now consists of the embryo sac and two surrounding integuments.

▼ Figure 38.4

## Exploring Flower Pollination

Most angiosperm species rely on a living (biotic) or nonliving (abiotic) pollinating agent that can move pollen from the anther of a flower on one plant to the stigma of a flower on another plant. Approximately 80% of all angiosperm pollination is biotic, employing animal go-betweens. Among abiotically pollinated species, 98% rely on wind and 2% on water. (Some angiosperm species can self-pollinate, but such species are limited to inbreeding in nature.)

### Abiotic Pollination by Wind

About 20% of all angiosperm species are wind-pollinated. Since their reproductive success does not depend on attracting pollinators, there has been no selective pressure favoring colorful or scented flowers. Accordingly, the flowers of wind-pollinated species are often small, green, and inconspicuous, and they produce neither nectar nor scent. Most temperate trees and grasses are wind-pollinated. The flowers of hazel (*Corylus avellana*, shown here) and many other temperate, wind-pollinated trees appear in the early spring, when leaves are not present to interfere with pollen movement. The relative inefficiency of wind pollination is compensated for by production of copious amounts of pollen grains. Wind tunnel studies reveal that wind pollination is often more efficient than it appears because floral structures can create eddy currents that aid in pollen capture.



▲ Hazel staminate flowers (stamens only)

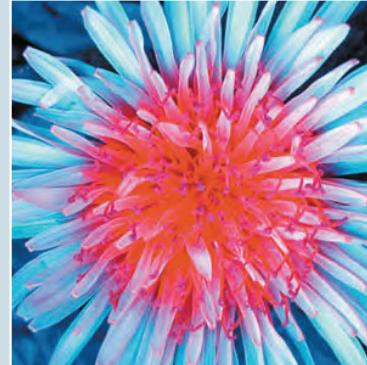
► Hazel carpellate flower (carpels only)

### Pollination by Bees

About 65% of all flowering plants require insects for pollination; the percentage is even greater for major crops. Bees are the most important insect pollinators, and there is great concern in Europe and North America that honeybee populations have shrunk. Pollinating bees depend on nectar and pollen for food. Typically, bee-pollinated flowers have a delicate, sweet fragrance. Bees are attracted to bright colors, primarily yellow and blue. Red appears dull to them, but they can see ultraviolet radiation. Many bee-pollinated flowers, such as the common dandelion (*Taraxacum vulgare*), have ultraviolet markings called “nectar guides” that help insects locate the nectaries (nectar-producing glands) but are only visible to human eyes under ultraviolet light.



▲ Common dandelion under normal light

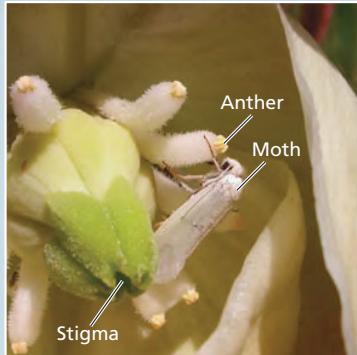


▲ Common dandelion under ultraviolet light

## Pollination

In angiosperms, **pollination** is the transfer of pollen from an anther to a stigma. It is accomplished by wind, water, or animals (**Figure 38.4**). In wind-pollinated species, including grasses and many trees, the release of enormous quantities of smaller-sized pollen compensates for the randomness of dispersal by the wind. At certain times of the year, the air is

loaded with pollen grains, as anyone who is plagued with pollen allergies can attest. Some species of aquatic plants rely on water to disperse pollen. Most angiosperm species, however, depend on insects, birds, or other animal pollinators to transfer pollen directly from one flower to another. If pollination is successful, a pollen grain produces a pollen tube, which then grows down into the ovary via the style.



▲ Moth on yucca flower



▲ Blowfly on carrion flower



▲ Long-nosed bat feeding on cactus flower at night

## Pollination by Moths and Butterflies

Moths and butterflies detect odors, and the flowers they pollinate are often sweetly fragrant. Butterflies perceive many bright colors, but moth-pollinated flowers are usually white or yellow, which stand out at night when moths are active. A yucca plant (shown here) is typically pollinated by a single species of moth with appendages that pack pollen onto the stigma. The moth then deposits eggs directly into the ovary. The larvae eat some developing seeds, but this cost is outweighed by the benefit of an efficient and reliable pollinator. If a moth deposits too many eggs, the flower aborts and drops off, selecting against individuals that overexploit the plant.

What are the benefits and dangers to a plant of having a highly specific animal pollinator?

## Pollination by Flies

Many fly-pollinated flowers are reddish and fleshy, with an odor like rotten meat. Blowflies visiting carrion flowers (*Stapelia* species) mistake the flower for a rotting corpse and lay their eggs on it. In the process, the blowflies become dusted with pollen that they carry to other flowers. When the eggs hatch, the larvae find no carrion to eat and therefore die.

## Pollination by Birds

Bird-pollinated flowers, such as columbine flowers, are usually large and bright red or yellow, but they have little odor. Since birds often do not have a well-developed sense of smell, there has been no selective pressure favoring scent production. However, the flowers produce the sugary solution called nectar that helps meet the high energy demands of the pollinating birds. The primary function of nectar, which is produced by nectaries at the base of many flowers, is to "reward" the pollinator. The petals of such flowers are often fused, forming a bent floral tube that fits the curved beak of the bird.



## Coevolution of Flower and Pollinator

**EVOLUTION** The joint evolution of two interacting species, each in response to selection imposed by the other, is called **coevolution**. Many species of flowering plants have co-evolved with specific pollinators. Natural selection favors individual plants or insects having slight deviations of structure that enhance the flower-pollinator mutualism. For example, some species have flower petals fused together, forming long, tube-like structures bearing nectaries tucked deep inside. Charles Darwin suggested that a race between flower and insect might lead to correspondences between the length of a floral tube and the length of an insect's proboscis, a straw-like mouthpart. Imagine an insect with a tongue long enough to drink the nectar of flowers without picking up pollen on its body. The resulting failure of these plants to fertilize others would render them less evolutionarily fit. Natural selection would then favor flowers with longer tubes. At the same time, an insect with a tongue that was too short for the tube wouldn't be able to use the nectar as a food source and therefore would be at a selective disadvantage compared with long-tongued rivals. As a result, the shapes and sizes of flowers often show a close correspondence to the pollen-adhering parts of their animal pollinators. In fact, based on the length of a long, tubular flower that grows in Madagascar, Darwin predicted the existence of a pollinating moth with a 28-cm-long proboscis. Such a moth was discovered two decades after Darwin's death (Figure 38.5).

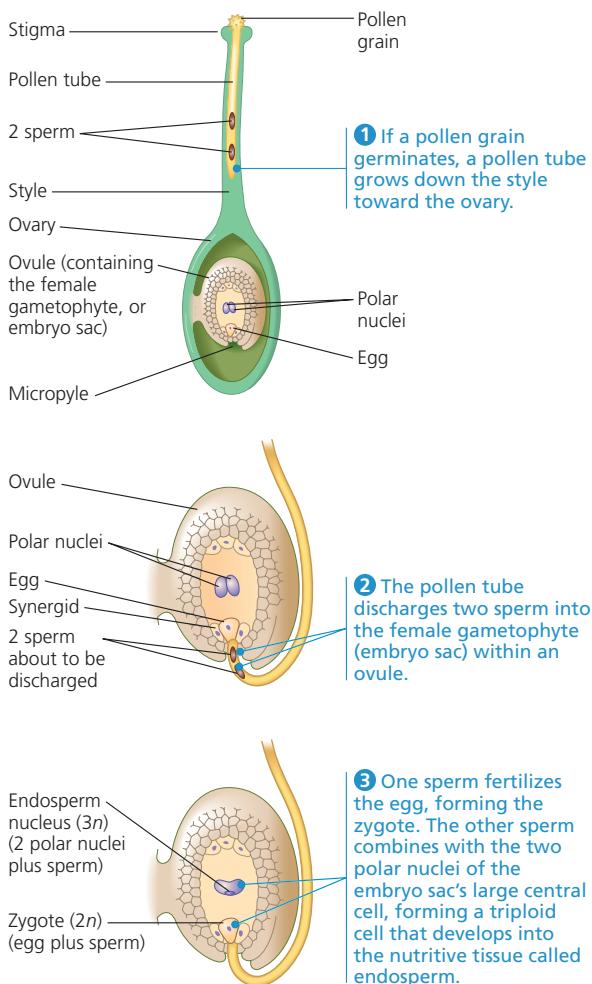


▲ **Figure 38.5 Coevolution of a flower and an insect pollinator.** The long floral tube of the Madagascar orchid *Angraecum sesquipedale* has coevolved with the 28-cm-long proboscis of its pollinator, the hawkmoth *Xanthopan morganii praedicta*. The moth is named in honor of Darwin's prediction of its existence.

## Double Fertilization

At the time of pollination, the pollen grain typically consists of only the tube cell and the generative cell. After a pollen grain lands on a suitable stigma, it absorbs water and germinates by producing a pollen tube, which grows between the cells of the style toward the ovary (Figure 38.6). The nucleus of the generative cell divides by mitosis and forms two sperm. In response to chemical attractants produced by the synergids, the tip of the pollen tube grows toward the micropyle. Its arrival initiates the death of one of the two synergids, thereby providing a passageway into the embryo sac for the two sperm that are discharged from the pollen tube.

Upon reaching the female gametophyte, one sperm fertilizes the egg, forming the zygote. The other sperm combines with the two polar nuclei, forming a triploid ( $3n$ ) nucleus in the



▲ **Figure 38.6 Growth of the pollen tube and double fertilization.**

center of the large central cell of the female gametophyte. This large cell will give rise to the **endosperm**, a food-storing tissue of the seed. The union of two sperm cells with different nuclei of the female gametophyte is called **double fertilization**. Double fertilization ensures that endosperm develops only in ovules where the egg has been fertilized, thereby preventing angiosperms from squandering nutrients on infertile ovules.

The tissues surrounding the female gametophyte have prevented researchers from directly observing fertilization in plants grown under normal conditions. Scientists have, however, isolated sperm from germinated pollen grains and eggs from female gametophytes and observed the merging of plant gametes *in vitro* (in an artificial environment). The first cellular event that takes place after gamete fusion is an increase in the levels of cytoplasmic calcium ions ( $\text{Ca}^{2+}$ ) in the egg, as also occurs during animal gamete fusion (see Chapter 47). Another similarity to animals is the establishment of a block to **polyspermy**, the fertilization of an egg by multiple sperm. Thus, sperm cannot fuse with zygotes even *in vitro*. In maize (*Zea mays*), for example, this barrier to polyspermy is established as early as 45 seconds after the initial fusion of sperm with egg.

### Seed Development, Form, and Function

After double fertilization, each ovule develops into a seed, and the ovary develops into a fruit enclosing the seed(s). As the embryo develops from the zygote, the seed stockpiles proteins, oils, and starch to varying degrees, depending on the species. This is why seeds are such a major nutrient drain. Initially, carbohydrates and other nutrients are stored in the seed's endosperm, but later, depending on the species, the swelling cotyledons (seed leaves) of the embryo may take over this function.

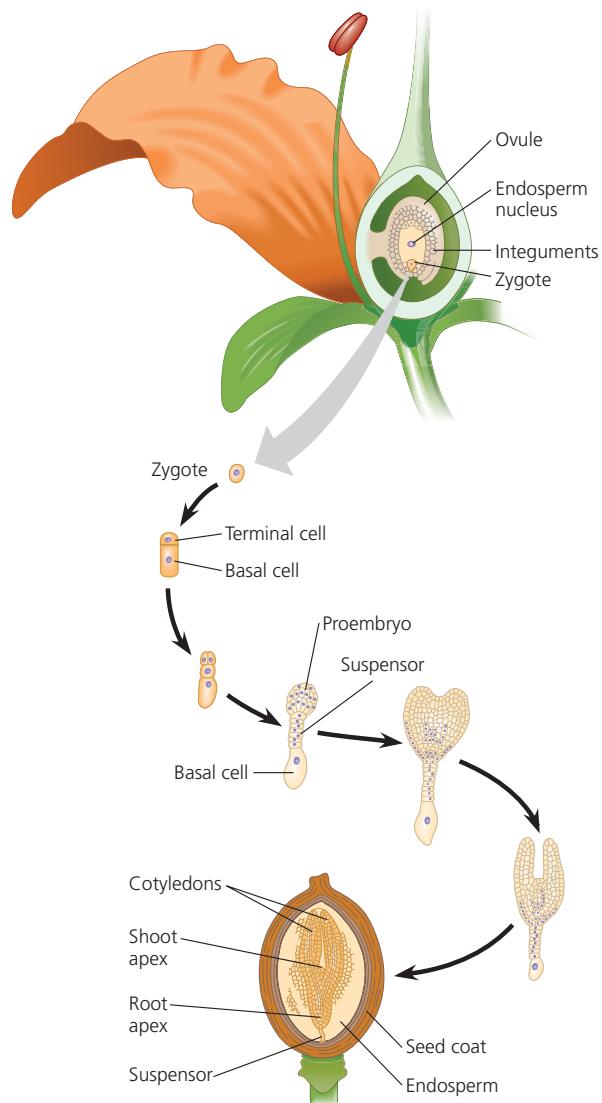
#### Endosperm Development

Endosperm usually develops before the embryo does. After double fertilization, the triploid nucleus of the ovule's central cell divides, forming a multinucleate "supercell" that has a milky consistency. This liquid mass, the endosperm, becomes multicellular when cytokinesis partitions the cytoplasm by forming membranes between the nuclei. Eventually, these "naked" cells produce cell walls, and the endosperm becomes solid. Coconut "milk" and "meat" are examples of liquid and solid endosperm, respectively. The white fluffy part of popcorn is also endosperm.

In grains and most other species of monocots, as well as many eudicots, the endosperm stores nutrients that can be used by the seedling after germination. In other eudicot seeds, the food reserves of the endosperm are completely exported to the cotyledons before the seed completes its development; consequently, the mature seed lacks endosperm.

#### Embryo Development

The first mitotic division of the zygote splits the fertilized egg into a basal cell and a terminal cell (Figure 38.7). The



**▲ Figure 38.7 The development of a eudicot plant embryo.**  
By the time the ovule becomes a mature seed and the integuments harden and thicken into the seed coat, the zygote has given rise to an embryonic plant with rudimentary organs.

terminal cell eventually gives rise to most of the embryo. The basal cell continues to divide, producing a thread of cells called the *suspensor*, which anchors the embryo to the parent plant. The suspensor helps in transferring nutrients to the embryo from the parent plant and, in some species of plants, from the endosperm. As the suspensor elongates, it pushes the embryo deeper into the nutritive and protective tissues. Meanwhile, the terminal cell divides several times and forms a spherical proembryo (early embryo) attached to the suspensor. The cotyledons begin to form as

bumps on the proembryo. A eudicot, with its two cotyledons, is heart-shaped at this stage. Only one cotyledon develops in monocots.

Soon after the rudimentary cotyledons appear, the embryo elongates. Cradled between the two cotyledons is the embryonic shoot apex. At the opposite end of the embryo's axis, where the suspensor attaches, an embryonic root apex forms. After the seed germinates—indeed, for the rest of the plant's life—the apical meristems at the apices of shoots and roots sustain primary growth (see Figure 35.11).

### Structure of the Mature Seed

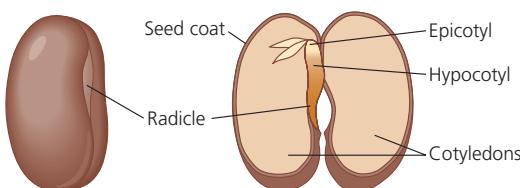
During the last stages of its maturation, the seed dehydrates until its water content is only about 5–15% of its weight. The embryo, which is surrounded by a food supply (cotyledons, endosperm, or both), enters **dormancy**; that is, it stops growing and its metabolism nearly ceases. The embryo and its food supply are enclosed by a hard, protective **seed coat** formed from the integuments of the ovule. In some species, dormancy is imposed by the presence of an intact seed coat rather than by the embryo itself.

You can take a closer look at one type of eudicot seed by splitting open the seed of a common garden bean. The embryo consists of an elongate structure, the embryonic axis, attached to fleshy cotyledons (Figure 38.8a). Below where the cotyledons are attached, the embryonic axis is called the **hypocotyl** (from the Greek *hypo*, under). The hypocotyl terminates in the **radicle**, or embryonic root. The portion of the embryonic axis above where the cotyledons are attached and below the first pair of miniature leaves is the **epicotyl** (from the Greek *epi*, on, over). The epicotyl, young leaves, and shoot apical meristem are collectively called the *plumule*.

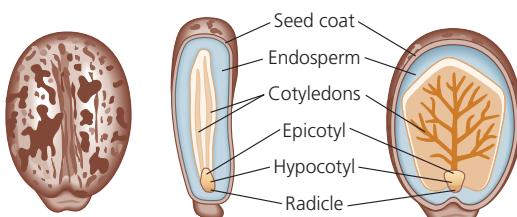
The cotyledons of the common garden bean are packed with starch before the seed germinates because they absorbed carbohydrates from the endosperm when the seed was developing. However, the seeds of some eudicot species, such as castor beans (*Ricinus communis*), retain their food supply in the endosperm and have very thin cotyledons (Figure 38.8b). The cotyledons absorb nutrients from the endosperm and transfer them to the rest of the embryo when the seed germinates.

The embryos of monocots possess only a single cotyledon (Figure 38.8c). Grasses, including maize and wheat, have a specialized cotyledon called a *scutellum* (from the Latin *scutella*, small shield, a reference to its shape). The scutellum, which has a large surface area, is pressed against the endosperm, from which it absorbs nutrients during germination. The embryo of a grass seed is enclosed within two protective sheathes: a **coleoptile**, which covers the young shoot, and a **coleorhiza**, which covers the young root. Both structures aid in soil penetration after germination.

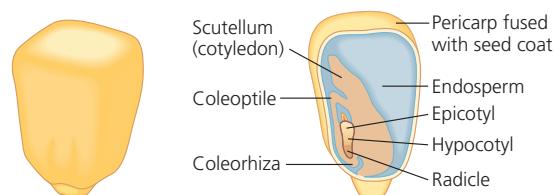
Seed weights range from less than 1 µg for some orchids to 20 kg for coco-de-mer palms. Orchid seeds have almost no



**(a) Common garden bean, a eudicot with thick cotyledons.** The fleshy cotyledons store food absorbed from the endosperm before the seed germinates.



**(b) Castor bean, a eudicot with thin cotyledons.** The narrow, membranous cotyledons (shown in edge and flat views) absorb food from the endosperm when the seed germinates.



**(c) Maize, a monocot.** Like all monocots, maize has only one cotyledon. Maize and other grasses have a large cotyledon called a scutellum. The rudimentary shoot is sheathed in a structure called the coleoptile, and the coleorhiza covers the young root.

▲ **Figure 38.8 Seed structure.**

**MAKE CONNECTIONS** In addition to cotyledon number, what are some other ways that the structures of monocots and eudicots differ? (See Figure 30.13 on p. 631.)

food reserves and must bond symbiotically with mycorrhizae prior to germination. Large, endosperm-rich palm seeds are an adaptation for seedling establishment on nutrient-poor beaches.

### Seed Dormancy: An Adaptation for Tough Times

Environmental conditions required to break seed dormancy vary among species. Seeds of some species germinate as soon as they are in a suitable environment. Others remain dormant, even if sown in a favorable place, until a specific environmental cue causes them to break dormancy.

The requirement for specific cues to break seed dormancy increases the chances that germination will occur at a time and place most advantageous to the seedling. Seeds of many desert plants, for instance, germinate only after a substantial rainfall. If they were to germinate after a mild drizzle, the soil

might soon become too dry to support the seedlings. Where natural fires are common, many seeds require intense heat or smoke to break dormancy; seedlings are therefore most abundant after fire has cleared away competing vegetation. Where winters are harsh, seeds may require extended exposure to cold. Seeds sown during summer or fall will then not germinate until the following spring, ensuring a long growth season before the next winter. Certain small seeds, such as those of some lettuce varieties, require light for germination and will break dormancy only if buried shallow enough for the seedlings to poke through the soil surface. Some seeds have coats that must be weakened by chemical attack as they pass through an animal's digestive tract and thus are usually carried a considerable distance before germinating from dropped feces.

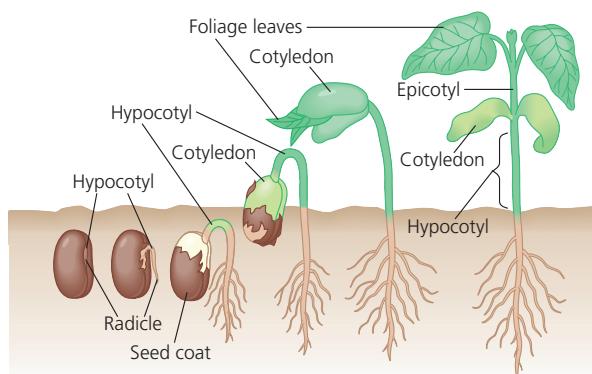
The length of time a dormant seed remains viable and capable of germinating varies from a few days to decades or even longer, depending on the plant species and environmental conditions. The oldest carbon-14-dated seed that has grown into a viable plant was a 2,000-year-old date palm seed recovered from excavations of Herod's palace in Israel. Most seeds are durable enough to last a year or two until conditions are favorable for germinating. Thus, the soil has a bank of ungerminated seeds that may have accumulated for several years. This is one reason vegetation reappears so rapidly after an environmental disruption such as fire.

### Seed Germination and Seedling Development

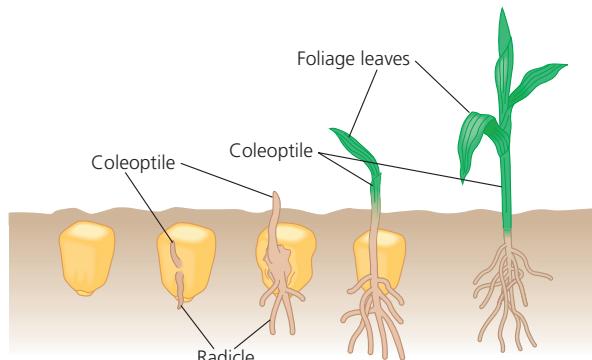
Germination depends on **imbibition**, the uptake of water due to the low water potential of the dry seed. Imbibing water causes the seed to expand and rupture its coat and also triggers metabolic changes in the embryo that enable it to resume growth. Following hydration, enzymes begin digesting the storage materials of the endosperm or cotyledons, and the nutrients are transferred to the growing regions of the embryo.

The first organ to emerge from the germinating seed is the radicle, the embryonic root. Next, the shoot tip must break through the soil surface. In garden beans and many other eudicots, a hook forms in the hypocotyl, and growth pushes the hook above ground (**Figure 38.9a**). In response to light, the hypocotyl straightens, the cotyledons separate, and the delicate epicotyl, now exposed, spreads its first true leaves (as distinct from the cotyledons, or seed leaves). These leaves expand, become green, and begin making food by photosynthesis. The cotyledons shrivel and fall away from the seedling, their food reserves having been exhausted by the germinating embryo.

Some monocots, such as maize and other grasses, use a different method for breaking ground when they germinate (**Figure 38.9b**). The coleoptile, the sheath enclosing and protecting the embryonic shoot, pushes upward through the soil and into the air. The shoot tip then grows straight up through the tunnel provided by the tubular coleoptile and eventually breaks out through the coleoptile's tip.



**(a) Common garden bean.** In common garden beans, straightening of a hook in the hypocotyl pulls the cotyledons from the soil.



**(b) Maize.** In maize and other grasses, the shoot grows straight up through the tube of the coleoptile.

### ▲ Figure 38.9 Two common types of seed germination.

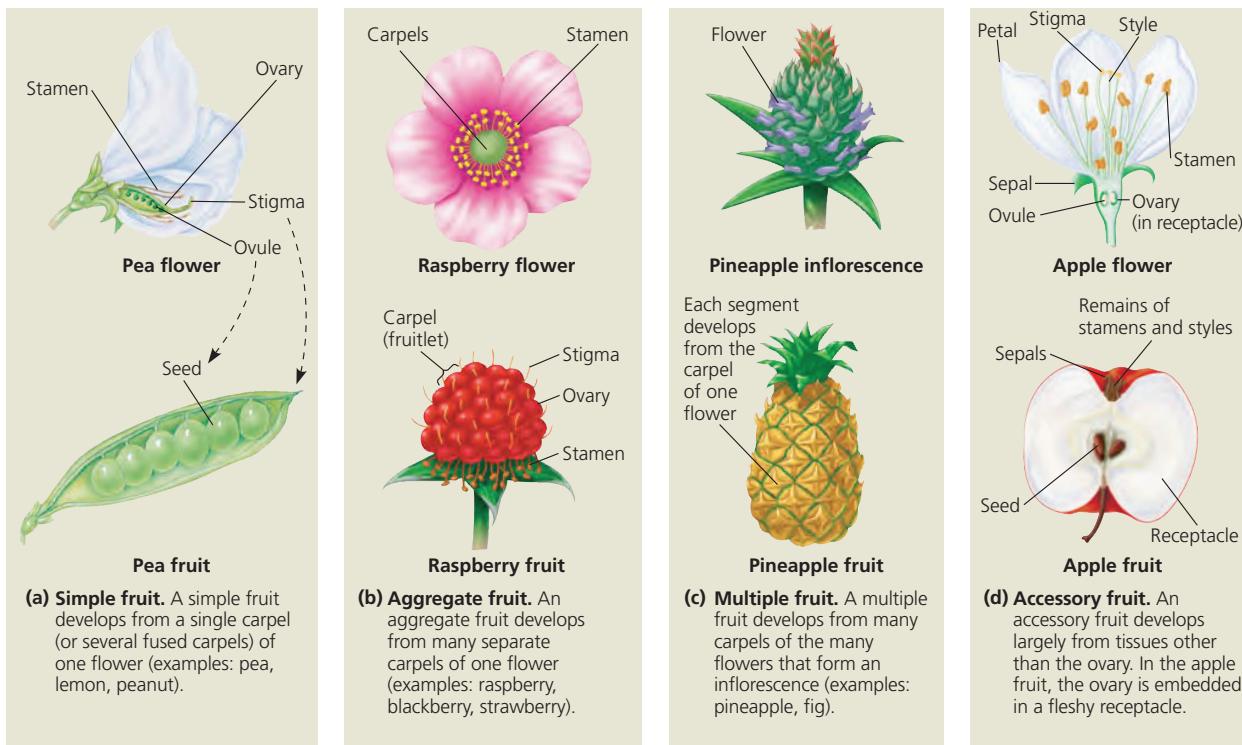
How do bean and maize seedlings protect their shoot systems as they push through the soil?

### Fruit Form and Function

While the seeds are developing from ovules, the ovary of the flower is developing into a **fruit**, which protects the enclosed seeds and, when mature, aids in their dispersal by wind or animals. Fertilization triggers hormonal changes that cause the ovary to begin its transformation into a fruit. If a flower has not been pollinated, fruit typically does not develop, and the entire flower usually withers and falls away.

During fruit development, the ovary wall becomes the pericarp, the thickened wall of the fruit. As the ovary grows, the other parts of the flower usually wither and are shed. For example, the pointed tip of a pea pod is the withered remains of the pea flower's stigma.

Fruits are classified into several types, depending on their developmental origin. Most fruits are derived from a single



▲ **Figure 38.10** Developmental origin of fruits.

carpel or several fused carpels and are called **simple fruits** (**Figure 38.10a**). Some simple fruits are dry, such as a pea pod or a nut, whereas others are fleshy, such as a nectarine (see Figure 30.8). An **aggregate fruit** results from a single flower that has more than one separate carpel, each forming a small fruit (**Figure 38.10b**). These “fruitlets” are clustered together on a single receptacle, as in a raspberry. A **multiple fruit** develops from an inflorescence, a group of flowers tightly clustered together. When the walls of the many ovaries start to thicken, they fuse together and become incorporated into one fruit, as in a pineapple (**Figure 38.10c**).

In some angiosperms, other floral parts contribute to what we commonly call the fruit. Such fruits are called **accessory fruits**. In apple flowers, the ovary is embedded in the receptacle, and the fleshy part of this simple fruit is derived mainly from the enlarged receptacle; only the apple core develops from the ovary (**Figure 38.10d**). Another example is the strawberry, an aggregate fruit consisting of an enlarged receptacle studded with tiny, partially embedded fruits, each bearing a single seed.

A fruit usually ripens about the same time that its seeds complete their development. Whereas the ripening of a dry fruit, such as a soybean pod, involves the aging and drying out of fruit tissues, the process in a fleshy fruit is more elaborate. Complex interactions of hormones result in an edible

fruit that entices animals that help disperse the seeds. The fruit’s “pulp” becomes softer as a result of enzymes digesting components of the cell walls. The color usually changes from green to another color, such as red, orange, or yellow. The fruit becomes sweeter as organic acids or starch molecules are converted to sugar, which may reach a concentration of as much as 20% in a ripe fruit. **Figure 38.11** examines some mechanisms of fruit dispersal in more detail.

In this section, you have learned about the unique features of sexual reproduction in angiosperms—flowers, fruits, and double fertilization. Next, we’ll examine asexual reproduction.

### CONCEPT CHECK 38.1

1. Distinguish between pollination and fertilization.
2. What is the benefit of seed dormancy?
3. **WHAT IF?** If flowers had shorter styles, pollen tubes would more easily reach the embryo sac. Suggest an explanation for why very long styles have evolved in most flowering plants.
4. **MAKE CONNECTIONS** Does the life cycle of animals have any structures analogous to plant gametophytes? Explain your answer. (See Figure 13.6 on p. 252.)

For suggested answers, see Appendix A.

▼ Figure 38.11

## Exploring Fruit and Seed Dispersal

A plant's life depends on finding fertile ground. But a seed that falls and sprouts beneath the parent plant will stand little chance of competing successfully for nutrients. To prosper, seeds must be widely dispersed. Plants use biotic dispersal agents as well as abiotic agents such as water and wind.

### Dispersal by Wind

► The winged seed of the tropical Asian climbing gourd *Alsomitra macrocarpa* glides through the air of the rain forest in wide circles when released.



▼ The winged fruit of a maple spins like a helicopter blade, slowing descent and increasing the chance of being carried farther by horizontal winds.



Dandelion fruit



► Tumbleweeds break off at the ground and tumble across the terrain, scattering their seeds.

▲ Some seeds and fruits are attached to umbrella-like "parachutes" that are made of intricately branched hairs and often produced in puffy clusters. These dandelion "seeds" (actually one-seeded fruits) are carried aloft by the slightest gust of wind.

### Dispersal by Animals



► The sharp, tack-like spines on the fruits of puncture vine (*Tribulus terrestris*) can pierce bicycle tires and injure animals, including humans. When these painful "tacks" are removed and discarded, the seeds are dispersed.



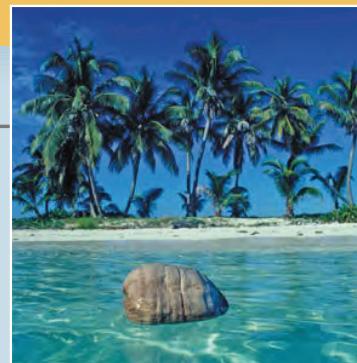
► Seeds in edible fruits are often dispersed in feces, such as the black bear feces shown here. Such dispersal may carry seeds far from the parent plant.



► Some animals, such as squirrels, hoard seeds or fruits in underground caches. If the animal dies or forgets the cache's location, the buried seeds are well positioned to germinate.



► Ants are chemically attracted to seeds with "food bodies" rich in fatty acids, amino acids, and sugars. The ants carry the seed to their underground nest, where the food body (the lighter-colored portion shown here) is removed and fed to larvae. Due to the seed's size, unwieldy shape, or hard coating, the remainder is usually left intact in the nest, where it germinates.



### Dispersal by Water

► Some buoyant seeds and fruits can survive months or years at sea. In coconut, the seed embryo and fleshy white "meat" (endosperm) are within a hard layer (endocarp) surrounded by a thick and buoyant fibrous husk.

## CONCEPT 38.2

### Flowering plants reproduce sexually, asexually, or both

Imagine chopping off your finger and watching it develop into an exact copy of you. If this could actually occur, it would be an example of **asexual reproduction**, in which offspring are derived from a single parent without fusion of egg and sperm. The result would be a clone, an asexually produced, genetically identical organism. Asexual reproduction is common in angiosperms, as well as in other plants, and for some plant species it is the predominant mode of reproduction.

#### Mechanisms of Asexual Reproduction

Asexual reproduction in plants is typically an extension of the capacity for indeterminate growth. As described in Concept 35.2, plant growth can be sustained or renewed indefinitely by meristems, regions of undifferentiated, dividing cells. In addition, parenchyma cells throughout the plant can divide and differentiate into more specialized types of cells, enabling plants to regenerate lost parts. Detached vegetative fragments of some plants can develop into whole offspring; for example, pieces of a potato with an “eye” (vegetative bud) can each regenerate a whole plant. Such **fragmentation**, the separation of a parent plant into parts that develop into whole plants, is one of the most common modes of asexual reproduction. The adventitious plantlets on *Kalanchoë* leaves exemplify an unusual type of fragmentation (see Figure 35.7). In other cases, the root system of a single parent, such as an aspen tree, can give rise to many adventitious shoots that become separate shoot systems (**Figure 38.12**). One aspen clone in Utah has been estimated to be composed of 47,000 stems of genetically

identical trees. Although it is likely that some of the root system connections have been severed, making some of the trees isolated from the rest of the clone, each tree still shares a common genome.

An entirely different mechanism of asexual reproduction has evolved in dandelions and some other plants. These plants can sometimes produce seeds without pollination or fertilization. This asexual production of seeds is called **apomixis** (from the Greek words meaning “away from the act of mixing”) because there is no joining or, indeed, production of sperm and egg. Instead, a diploid cell in the ovule gives rise to the embryo, and the ovules mature into seeds, which in the dandelion are dispersed by windblown fruits. Thus, these plants clone themselves by an asexual process but have the advantage of seed dispersal, usually associated with sexual reproduction. Introducing apomixis into hybrid crops is of great interest to plant breeders because apomixis would allow hybrid plants to pass on their desirable genomes intact to their offspring.

#### Advantages and Disadvantages of Asexual Versus Sexual Reproduction

An advantage of asexual reproduction is that there is no need for a pollinator. This may be beneficial in situations where plants of the same species are sparsely distributed and unlikely to be visited by the same pollinator. Asexual reproduction also allows the plant to pass on all of its genetic legacy intact to its progeny. In contrast, when reproducing sexually, a plant passes on only half of its alleles. If a plant is superbly suited to its environment, asexual reproduction can be advantageous. A vigorous plant can potentially clone many copies of itself, and if the environmental circumstances remain stable, these offspring will also be genetically well adapted to the same environmental conditions under which the parent flourished.

Generally, the progeny produced by asexual reproduction are stronger than seedlings produced by sexual reproduction. The offspring usually arise from mature vegetative fragments from the parent plant, which is why asexual reproduction in plants is also known as **vegetative reproduction**. In contrast, seed germination is a precarious stage in a plant’s life. The tough seed gives rise to a fragile seedling that may face exposure to predators, parasites, wind, and other hazards. In the wild, only a small fraction of seedlings survive to become parents themselves. Production of enormous numbers of seeds compensates for the odds against individual survival and gives natural selection ample genetic variations to screen. However, this is an expensive means of reproduction in terms of the resources consumed in flowering and fruiting.

Because sexual reproduction generates variation in offspring and populations, it can be advantageous in unstable environments where evolving pathogens and other fluctuating conditions affect survival and reproductive success. In contrast, the genotypic uniformity of asexually produced plants puts them at great risk of local extinction if there is a



▲ **Figure 38.12 Asexual reproduction in aspen trees.** Some aspen groves, such as those shown here, consist of thousands of trees descended by asexual reproduction. Each grove of trees derives from the root system of one parent. Thus, the grove is a clone. Notice that genetic differences between groves descended from different parents result in different timing for the development of fall color.

catastrophic environmental change, such as a new strain of disease. Moreover, seeds (which are almost always produced sexually) facilitate the dispersal of offspring to more distant locations. Finally, seed dormancy allows growth to be suspended until environmental conditions become more favorable.

Although sexual reproduction involving two genetically different plants has the benefit of producing the most genetically diverse offspring, some plants, such as garden peas, usually self-fertilize. This process, called “selfing,” can be a desirable attribute in some crop plants because it ensures that every ovule will develop into a seed. In many angiosperm species, however, mechanisms have evolved that make it difficult or impossible for a flower to fertilize itself, as we’ll discuss next.

### Mechanisms That Prevent Self-Fertilization

The various mechanisms that prevent self-fertilization contribute to genetic variety by ensuring that the sperm and egg come from different parents. In the case of **dioecious** species, plants cannot self-fertilize because different individuals have either staminate flowers (lacking carpels) or carpellate flowers (lacking stamens) (Figure 38.13a). Other plants have flowers with functional stamens and carpels that mature at different times or are structurally arranged in such a way that it is unlikely that an animal pollinator could transfer pollen from an

anther to a stigma of the same flower (Figure 38.13b). However, the most common anti-selfing mechanism in flowering plants is **self-incompatibility**, the ability of a plant to reject its own pollen and sometimes the pollen of closely related individuals. If a pollen grain lands on a stigma of a flower on the same plant, a biochemical block prevents the pollen from completing its development and fertilizing an egg.

Researchers are unraveling the molecular mechanisms involved in self-incompatibility. This plant response is analogous to the immune response of animals in that both are based on the ability to distinguish the cells of “self” from those of “non-self.” The key difference is that the animal immune system rejects nonself, as when the system mounts a defense against a pathogen or rejects a transplanted organ (see Chapter 43). Self-incompatibility in plants, in contrast, is a rejection of self.

Recognition of “self” pollen is based on genes for self-incompatibility, called *S*-genes. In the gene pool of a plant population, there can be dozens of alleles of an *S*-gene. If a pollen grain has an allele that matches an allele of the stigma on which it lands, the pollen tube fails to grow. Depending on the species, self-recognition blocks pollen tube growth by one of two molecular mechanisms: gametophytic self-incompatibility or sporophytic self-incompatibility.

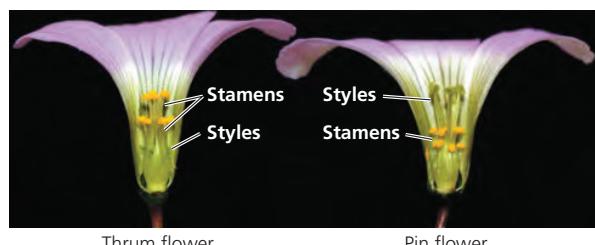
In gametophytic self-incompatibility, the *S*-allele in the pollen genome governs the blocking of fertilization. For example, an *S*<sub>1</sub> pollen grain from an *S*<sub>1</sub>*S*<sub>2</sub> parental sporophyte cannot fertilize eggs of an *S*<sub>1</sub>*S*<sub>2</sub> flower but can fertilize an *S*<sub>2</sub>*S*<sub>3</sub> flower. An *S*<sub>2</sub> pollen grain cannot fertilize either flower. Self-recognition of this kind involves the enzymatic destruction of RNA within a pollen tube. RNA-hydrolyzing enzymes are produced by the style and enter the pollen tube. If the pollen tube is a “self” type, these enzymes destroy its RNA.

In sporophytic self-incompatibility, fertilization is blocked by *S*-allele gene products in tissues of the parental sporophyte that adhere to the pollen grain wall. For example, neither an *S*<sub>1</sub> nor *S*<sub>2</sub> pollen grain from an *S*<sub>1</sub>*S*<sub>2</sub> parental sporophyte can fertilize eggs of an *S*<sub>1</sub>*S*<sub>2</sub> flower or *S*<sub>2</sub>*S*<sub>3</sub> flower, due to the *S*<sub>1</sub>*S*<sub>2</sub> parental tissue attached to the pollen wall. Sporophytic incompatibility involves a signal transduction pathway in epidermal cells of the stigma that prevents germination of the pollen grain.

Some crops, such as peas, maize, and tomatoes, routinely self-fertilize with satisfactory results. However, plant breeders frequently hybridize different varieties of a crop plant to combine the best traits of the varieties and counter the loss of vigor that can often result from excessive inbreeding. To obtain hybrid seeds, plant breeders today must prevent self-fertilization either by laboriously removing the anthers from the parent plants that provide the seeds (as Mendel did) or by developing male-sterile plants. The latter option is increasingly common. Eventually, it may also be possible to impose self-incompatibility genetically on crop species that are normally self-compatible. Basic research on mechanisms of self-incompatibility may thus have agricultural applications.



(a) Some species, such as *Sagittaria latifolia* (common arrowhead), are dioecious, having plants that produce only staminate flowers (left) or carpellate flowers (right).



(b) Some species, such as *Oxalis alpina* (alpine wood sorrel), produce two types of flowers on different individuals: “thrums,” which have short styles and long stamens, and “pins,” which have long styles and short stamens. An insect foraging for nectar would collect pollen on different parts of its body; thrum pollen would be deposited on pin stigmas, and vice versa.

▲ **Figure 38.13** Some floral adaptations that prevent self-fertilization.

## Vegetative Propagation and Agriculture

With the objective of improving crops and ornamental plants, humans have devised various methods for asexual propagation of angiosperms. Most of these methods are based on the ability of plants to form adventitious roots or shoots.

### Clones from Cuttings

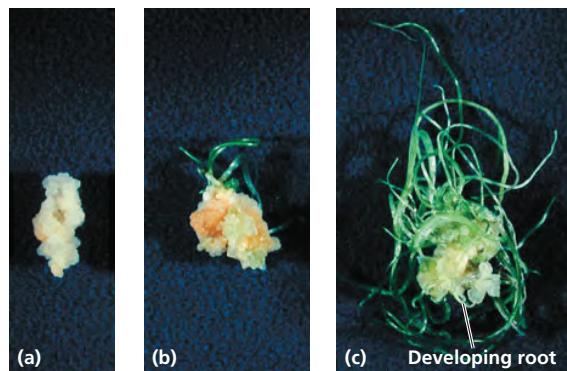
Most houseplants, woody ornamentals, and orchard trees are asexually reproduced from plant fragments called cuttings. In some cases, shoot cuttings are used. At the cut end of the shoot, a mass of dividing, undifferentiated cells called a **callus** forms, and adventitious roots then develop from the callus. If the shoot fragment includes a node, then adventitious roots form without a callus stage. Some plants, including African violets, can be propagated from single leaves rather than stems. For other plants, cuttings are taken from specialized storage stems, such as potato tubers. The Bartlett pear and the Red Delicious apple are examples of varieties that have been propagated asexually for over 150 years.

### Grafting

In a modification of vegetative reproduction from cuttings, a twig or bud from one plant can be grafted onto a plant of a closely related species or a different variety of the same species. Grafting makes it possible to combine the best qualities of different species or varieties into a single plant. The plant that provides the root system is called the **stock**; the twig grafted onto the stock is referred to as the **scion**. For example, scions from French varieties of vines that produce superior wine grapes are grafted onto rootstocks of American varieties that produce inferior grapes but are more resistant to certain soil pathogens. The genes of the scion determine the quality of the fruit.

### Test-Tube Cloning and Related Techniques

Plant biologists have adopted *in vitro* methods to clone novel plant varieties. They can grow whole plants by culturing small pieces of tissue from the parent plant on an artificial medium containing nutrients and hormones. The cells or tissues can come from any part of a plant, but growth may vary depending on the plant part, species, and artificial medium. In some media, the cultured cells divide and form a callus of undifferentiated cells (**Figure 38.14a**). When the concentrations of hormones and nutrients are manipulated appropriately, a callus can sprout shoots and roots with fully differentiated cells (**Figure 38.14b,c**). The plantlets can then be transferred to soil, where they continue their growth. A single plant can be cloned into thousands of copies by dividing calluses as they grow. This method is now used for propagating orchids as well as a wide variety of trees and shrubs.



▲ **Figure 38.14** Cloning a garlic plant. (a) A root from a garlic clove gave rise to this callus culture, a mass of undifferentiated cells. (b and c) The differentiation of a callus into a plantlet depends on the nutrient levels and hormone concentrations in the artificial medium, as can be seen in these cultures grown for different lengths of time.

Plant tissue culture also facilitates genetic engineering. Most techniques for the introduction of foreign genes into plants require small pieces of plant tissue or single plant cells as the starting material. The term **transgenic** is used to describe genetically modified (GM) organisms that have been engineered to express a gene from another species. Test-tube culture makes it possible to regenerate GM plants from a single plant cell into which the foreign DNA has been incorporated. The techniques of genetic engineering are discussed in more detail in Chapter 20.

Some researchers couple a technique known as **protoplast fusion** with tissue culture methods to invent new plant varieties that can be cloned. Protoplasts are plant cells with their cell walls removed by treatment with enzymes (cellulases and pectinases) isolated from fungi (**Figure 38.15**). In some cases, it is possible to fuse two protoplasts from different plant species that would otherwise be reproductively incompatible and then culture the hybrid protoplasts. Each protoplast can regenerate a wall and eventually form a hybrid plantlet. The hybrid produced by the protoplast fusion



◀ **Figure 38.15** Protoplasts.

These plant cells without walls are prepared by treating cells or tissues with wall-degrading enzymes isolated from certain fungi. Researchers can fuse protoplasts from different species to make hybrid cells and can then culture the cells to produce a new plant (LM).

of two *Datura* species, for example, produces fertile seeds and is considered a new species. This hybrid can grow larger than the two parent species and is about 25% richer in medicinal alkaloids.

The *in vitro* culturing of plant cells and tissues is fundamental to most types of plant biotechnology. The other basic process is the production of transgenic plants through various methods of genetic engineering. In the next section, we take a closer look at plant biotechnology.

### CONCEPT CHECK 38.2

1. The seedless banana, the world's most popular fruit, is losing the battle against two fungal epidemics. Why do such epidemics generally pose a greater risk to asexually propagated crops?
2. Self-fertilization, or selfing, seems to have obvious disadvantages as a reproductive "strategy" in nature, and it has even been called an "evolutionary dead end." So it is surprising that about 20% of angiosperm species primarily rely on selfing. Suggest a reason why selfing might be advantageous and yet still be an evolutionary dead end.
3. **WHAT IF?** Potatoes (*Solanum tuberosum*) and tomatoes (*Solanum lycopersicum*) are fairly closely related species. If you managed to cross the two, would it be possible to have a hybrid that makes potato-like tubers and tomato-like fruits on the same plant?

For suggested answers, see Appendix A.

### CONCEPT 38.3

#### Humans modify crops by breeding and genetic engineering

Humans have intervened in the reproduction and genetic makeup of plants since the dawn of agriculture. As explained by Luis Herrera-Estrella in the Unit Six interview (see pp. 736–737), maize owes its existence to humans. Left on its own in nature, maize would soon become extinct for the simple reason that it cannot spread its seeds. Maize kernels are not only permanently attached to the central axis (the "cob") but also permanently protected by tough, overlapping leaf sheathes (the "husk") (Figure 38.16). These attributes arose by artificial selection by humans. (See Chapter 22 to review the basic concept of artificial selection.) Despite having no understanding of the scientific principles underlying plant breeding, Neolithic (late Stone Age) humans domesticated most of our crop species over a relatively short period about 10,000 years ago. But genetic modification began long before humans started altering crops by artificial selection. For example,



▲ Figure 38.16 Maize: a product of artificial selection.

Modern maize (bottom) was derived from teosinte (top). Teosinte kernels are tiny, and each row has a husk that must be removed to get at the kernel. The seeds are loose at maturity, allowing dispersal, which probably made harvesting difficult for early farmers. Neolithic farmers selected seeds from plants with larger cob and kernel size as well as the permanent attachment of seeds to the cob and the encasing of the entire cob by a tough husk.

the wheat species we rely on for much of our food evolved by the natural hybridization between different species of grasses. Such hybridization is common in plants and has long been exploited by breeders to introduce genetic variation for artificial selection and crop improvement.

#### Plant Breeding

The art of recognizing valuable traits is important in plant breeding. Breeders scrutinize their fields carefully and travel to other countries searching for domesticated varieties or wild relatives with desirable traits. Such traits occasionally arise spontaneously through mutation, but the natural rate of mutation is too slow and unreliable to produce all the mutations that breeders would like to study. Breeders sometimes hasten mutations by treating large batches of seeds or seedlings with radiation or chemicals.

When a desirable trait is identified in a wild species, the wild species is crossed with a domesticated variety. Generally, those progeny that have inherited the desirable trait from the wild parent have also inherited many traits that are not desirable for agriculture, such as small fruits or low yields. The progeny that express the desired trait are again crossed with members of the domesticated species and their progeny examined for the desired trait. This process is continued until the progeny with the desired wild trait resemble the original domesticated parent in their other agricultural attributes.

While most breeders cross-pollinate plants of a single species, some breeding methods rely on hybridization between two distant species of the same genus. Such crosses often result in the abortion of the hybrid seed during development. Very often the embryo begins to develop, but the endosperm does not. Hybrid embryos are sometimes rescued

by surgically removing them from the ovule and culturing them *in vitro*.

Less commonly, hybridization is carried out on members of two different genera. A cross between wheat (*Triticum aestivum*) and rye (*Secale cereale*), for example, produced a novel grain called triticale, which contains a copy of all the chromosomes from both species. When triticale was first produced in the 1870s, it was considered little more than a botanical oddity. In the mid-1900s, however, plant breeders realized that triticale could potentially be developed into a crop with the yield and quality of bread wheat and with rye's tolerance of cold stress, moisture stress, and acidic soils. The early triticales were plagued with problems. These tall, late-maturing plants tended to fall over, were partially sterile, and were low yielding. They typically produced shriveled seeds that germinated poorly and were of poor quality for milling and baking. But through continued artificial selection, these problems were overcome, and triticale is now grown worldwide on more than 1 million hectares of marginal (poor-quality) farmland (1 ha = 2.47 acres). If we are to feed the rapidly growing world population in the 21st century, such marginal lands will have to become increasingly productive.

## Plant Biotechnology and Genetic Engineering

Plant biotechnology has two meanings. In the general sense, it refers to innovations in the use of plants (or substances obtained from plants) to make products of use to humans—an endeavor that began in prehistory. In a more specific sense, biotechnology refers to the use of GM organisms in agriculture and industry. Indeed, in the last two decades, genetic engineering has become such a powerful force that the terms *genetic engineering* and *biotechnology* have become synonymous in the media.

Unlike traditional plant breeders, modern plant biotechnologists, using techniques of genetic engineering, are not limited to the transfer of genes between closely related species or genera. For example, traditional breeding techniques could not be used to insert a desired gene from daffodil into rice because the many intermediate species between rice and daffodil and their common ancestor are extinct. In theory, if breeders had the intermediate species, over the course of several centuries they could probably introduce a daffodil gene into rice by traditional hybridization and breeding methods. With genetic engineering, however, such gene transfers can be done more quickly, more specifically, and without the need for intermediate species.

In the remainder of this chapter, we expand on discussions in Chapter 20 by examining the prospects and controversies surrounding the use of GM crops. The advocates of plant biotechnology believe that the genetic engineering of crop plants is the key to overcoming some of the most

pressing problems of the 21st century, including world hunger and fossil fuel dependency.

### Reducing World Hunger and Malnutrition

Currently, 800 million people suffer from nutritional deficiencies, with 40,000 dying each day of malnutrition, half of them children. There is much disagreement about the causes of such hunger. Some argue that food shortages arise from inequities in distribution and that the dire poor simply cannot afford food. Others regard food shortages as evidence that the world is overpopulated—that the human species has exceeded the carrying capacity of the planet (see Chapter 53). Whatever the social and demographic causes of malnutrition, increasing food production is a humane objective. Because land and water are the most limiting resources, the best option is to increase yields on already existing farmland. Indeed, there is very little “extra” land that can be farmed, especially if the few remaining pockets of wilderness are to be preserved. Based on conservative estimates of population growth, farmers will have to produce 40% more grain per hectare to feed the human population in 2030. Plant biotechnology can help make these crop yields possible.

The commercial use of transgenic crops has been one of the most dramatic examples of rapid technology adoption in the history of agriculture. These crops include varieties and hybrids of cotton, maize, and potatoes that contain genes from the bacterium *Bacillus thuringiensis*. These “transgenes” encode a protein (*Bt* toxin) that is toxic to insect pests. The use of such plant varieties greatly reduces the need for chemical insecticides. The *Bt* toxin used in crops is produced in the plant as a harmless protoxin that only becomes toxic if activated by alkaline conditions, such as occur in the guts of insects. Because vertebrates have highly acidic stomachs, protoxin consumed by humans or farm animals is destroyed without becoming active.

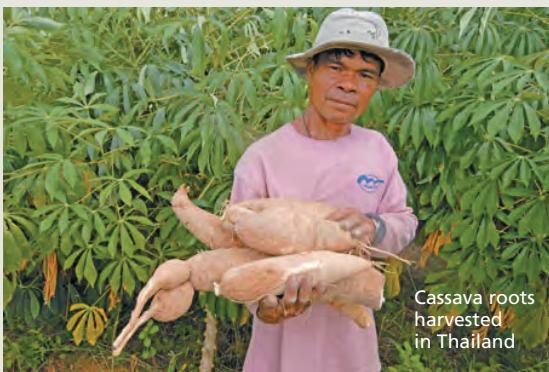
Considerable progress has also been made in developing transgenic crops that tolerate certain herbicides. The cultivation of these plants may reduce production costs by enabling farmers to “weed” crops with herbicides that do not damage the transgenic crop plants, instead of using heavy tillage, which can cause soil erosion. Researchers are also engineering plants with enhanced resistance to disease. In one case, a transgenic papaya resistant to a ring spot virus was introduced into Hawaii, thereby saving its papaya industry.

The nutritional quality of plants is also being improved. For example, some 250,000 to 500,000 children go blind each year because of vitamin A deficiencies. More than half of these children die within a year of becoming blind. In response to this crisis, genetic engineers have created “Golden Rice,” a transgenic variety supplemented with two daffodil genes that enable it to produce grain containing beta-carotene, a precursor of vitamin A. Another target for improvement by genetic

▼ **Figure 38.17**  
**IMPACT**

### Fighting World Hunger with Transgenic Cassava

Plant biologists are racing to mold cassava (*Manihot esculenta*) into the perfect food. This starchy root crop is plentiful and easy to grow and is the primary food for 800 million of the world's poor. But it has several drawbacks. Composed almost entirely of carbohydrates, it provides plenty of calories but not a complete and balanced diet. Moreover, it must be processed to remove chemicals that release cyanide, and workers can be sickened by chronic exposure to this toxin. However, transgenic cassava plants have been developed with greatly enriched levels of protein, iron, and beta-carotene (a vitamin A precursor), and cyanide-producing chemicals have been almost eliminated from the roots. Researchers have also created cassava plants with root masses twice the normal size.



**WHY IT MATTERS** Feeding the world's hungry will continue to be a daunting challenge in the 21st century because their population continues to climb. Untold human misery can be avoided if plant biologists can produce a cassava variety so nutritious that a 500-gram serving a day will provide a full and healthy diet.

**FURTHER READING** N. Nassar and R. Ortiz, Breeding cassava to feed the poor, *Scientific American* 302:78–84 (2010).

**MAKE CONNECTIONS** Genetic transformation using *Agrobacterium tumefaciens*, which causes crown gall disease, is the preferred method for transporting new genes into cassava cells. Review Concept 20.4, page 421, and explain why the use of this pathogen in genetic engineering does not produce crown gall disease in transgenic plants.

engineering is cassava, a staple for 800 million of the poorest people on our planet (Figure 38.17).

#### Reducing Fossil Fuel Dependency

Global sources of inexpensive fossil fuels, particularly oil, are rapidly being depleted. Moreover, most climatologists attribute global warming mainly to the rampant burning of fossil fuels, such as coal and oil, and the resulting release of the greenhouse gas CO<sub>2</sub>. How can the world meet its energy demands in the 21st century in an economical and nonpolluting way? In

certain localities, wind or solar power may become economically viable, but such alternative energy sources are unlikely to fill the global energy demands completely. Many scientists predict that biomass from extremely fast-growing plants, such as switchgrass (*Panicum virgatum*) and poplar (*Populus trichocarpa*), could produce a sizable fraction of the world's energy needs in the not-too-distant future.

Under optimal conditions, poplars can grow 3–4 m each year, and switchgrass grows well under a wide variety of conditions found in regions where most types of agriculture are not economically viable. Scientists do not envisage the plant biomass being burned directly. Instead, the polymers in cell walls, such as cellulose and hemicellulose, which constitute the most abundant organic compounds on Earth, would be broken down into sugars by enzymatic reactions. These sugars, in turn, would be fermented into alcohol and distilled to yield **biofuels**.

The use of biofuels from plant biomass would reduce the net emission of CO<sub>2</sub>. Whereas burning fossil fuels increases atmospheric CO<sub>2</sub> concentrations, biofuel crops reabsorb by photosynthesis the CO<sub>2</sub> emitted when biofuels are burned, creating a cycle that is carbon neutral. Plant breeders are trying to genetically engineer faster-growing poplar trees that produce more readily convertible biomass.

Biofuel technology does have its critics. For example, ecologist David Pimentel, of Cornell University, and geoengineer Tad Patzek, of the University of California, Berkeley, have estimated that more energy may be required to produce biofuels than would be produced from combustion of these products. Biofuel advocates, in turn, have questioned the accuracy of the data underlying these estimates.

#### The Debate over Plant Biotechnology

Much of the debate about GM organisms (GMOs) in agriculture is political, social, economic, or ethical and therefore outside the scope of this book. But we *should* consider the biological concerns about GM crops. Some biologists, particularly ecologists, are concerned about the unknown risks associated with the release of GMOs into the environment. The debate centers on the extent to which GMOs could harm the environment or human health. Those who want to proceed more slowly with agricultural biotechnology (or end it) are concerned about the unstoppable nature of the “experiment.” If a drug trial produces unanticipated harmful results, the trial is stopped. But we may not be able to stop the “trial” of introducing novel organisms into the biosphere.

Chapter 20 introduced the key concerns regarding biotechnology in general. Here we take a closer look at some issues as they relate to plant biotechnology. Laboratory and field studies continue to examine the possible consequences of using GM crops, including the effects on human health and non-target organisms and the potential for transgene escape.

### Issues of Human Health

Many GMO opponents worry that genetic engineering may inadvertently transfer allergens, molecules to which some people are allergic, from a species that produces an allergen to a plant used for food. However, biotechnologists are already engaged in removing genes that encode allergenic proteins from soybeans and other crops. So far, there is no credible evidence that GM plants specifically designed for human consumption have adverse effects on human health. In fact, some GM foods are potentially healthier than non-GM foods. For example, *Bt* maize (the transgenic variety with the *Bt* toxin) contains 90% less of a cancer-causing and birth defect-causing fungal toxin than non-*Bt* maize. Called fumonisin, this toxin is highly resistant to degradation and has been found in alarmingly high concentrations in some batches of processed maize products, ranging from cornflakes to beer. Fumonisin is produced by a fungus (*Fusarium*) that infects insect-damaged maize. Because *Bt* maize generally suffers less insect damage than non-GM maize, it contains much less fumonisin.

Nevertheless, because of health concerns, GMO opponents lobby for the clear labeling of all foods containing products of GMOs. Some also argue for strict regulations against the mixing of GM foods with non-GM foods during food transport, storage, and processing. Biotechnology advocates, however, note that similar demands were not made when “transgenic” crops produced by traditional plant-breeding techniques were put on the market. There are, for example, some commercially grown varieties of wheat derived by traditional plant-breeding techniques that contain entire chromosomes (and thousands of genes) from rye.

### Possible Effects on Nontarget Organisms

Many ecologists are concerned that the growing of GM crops might have unforeseen effects on nontarget organisms. One laboratory study indicated that the larvae (caterpillars) of monarch butterflies responded adversely and even died after eating milkweed leaves (their preferred food) heavily dusted with pollen from transgenic *Bt* maize. This study has since been discredited, affording a good example of the self-correcting nature of science. As it turns out, when the original researchers shook the male maize inflorescences onto the milkweed leaves in the laboratory, the filaments of stamens, opened microsporangia, and other floral parts also rained onto the leaves. Subsequent research found that it was these other floral parts, *not* the pollen, that contained *Bt* toxin in high concentrations. Unlike pollen, these floral parts would not be carried by the wind to neighboring milkweed plants when shed under natural field conditions. Only one *Bt* maize line, accounting for less than 2% of commercial *Bt* maize production (and now discontinued), produced pollen with high *Bt* toxin concentrations.

In considering the negative effects of *Bt* pollen on monarch butterflies, one must also weigh the effects of an alternative to the cultivation of *Bt* maize—the spraying of non-*Bt* maize with chemical pesticides. Recent studies have shown that such spraying is much more harmful to nearby monarch populations than is *Bt* maize production. Although the effects of *Bt* maize pollen on monarch butterfly larvae appear to be minor, the controversy has emphasized the need for accurate field testing of all GM crops and the importance of targeting gene expression to specific tissues to improve safety.

### Addressing the Problem of Transgene Escape

Perhaps the most serious concern raised about GM crops is the possibility of the introduced genes escaping from a transgenic crop into related weeds through crop-to-weed hybridization. The fear is that the spontaneous hybridization between a crop engineered for herbicide resistance and a wild relative might give rise to a “superweed” that would have a selective advantage over other weeds in the wild and would be much more difficult to control in the field. Some crops do hybridize with weedy relatives, and crop-to-weed transgene escape is a possibility. Its likelihood depends on the ability of the crop and weed to hybridize and on how the transgenes affect the overall fitness of the hybrids. A desirable crop trait—a dwarf phenotype, for example—might be disadvantageous to a weed growing in the wild. In other instances, there are no weedy relatives nearby with which to hybridize; soybean, for example, has no wild relatives in the United States. However, canola, sorghum, and many other crops do hybridize readily with weeds.

Many different strategies are being pursued with the goal of preventing transgene escape. For example, if male sterility could be engineered into plants, these plants would still produce seeds and fruit if pollinated by nearby nontransgenic plants, but they would produce no viable pollen. A second approach involves genetically engineering apomixis into transgenic crops. When a seed is produced by apomixis, the embryo and endosperm develop without fertilization. The transfer of this trait to transgenic crops would therefore minimize the possibility of transgene escape via pollen because plants could be male-sterile without compromising seed or fruit production. A third approach is to engineer the transgene into the chloroplast DNA of the crop. Chloroplast DNA in many plant species is inherited strictly from the egg, so transgenes in the chloroplast cannot be transferred by pollen (see Chapter 15 to review maternal inheritance). A fourth approach for preventing transgene escape is to genetically engineer flowers that develop normally but fail to open. Consequently, self-pollination would occur, but pollen would be unlikely to escape from the flower. This solution would require modifications to flower design. Several floral genes have been identified that could be manipulated to this end.

The continuing debate about GMOs in agriculture exemplifies one of this textbook's recurring ideas: the relationship of science and technology to society. Technological advances almost always involve some risk of unintended outcomes. In plant biotechnology, zero risk is probably unattainable. Therefore, scientists and the public must assess on a case-by-case basis the possible benefits of transgenic products versus the risks that society is willing to take. The best scenario is for these discussions and decisions to be based on sound scientific information and rigorous testing rather than on reflexive fear or blind optimism.

### CONCEPT CHECK 38.3

1. Compare traditional plant-breeding methods with genetic engineering.
2. Explain some benefits and risks of GM crops.
3. Why does *Bt* maize have less fumonisin than non-GM maize?
4. **WHAT IF?** In a few species, chloroplast genes are inherited only from sperm. How might this influence efforts to prevent transgene escape?

For suggested answers, see Appendix A.

## 38 CHAPTER REVIEW

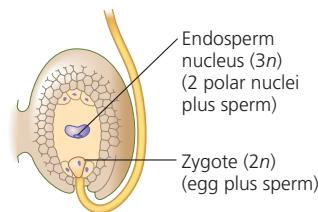
### SUMMARY OF KEY CONCEPTS

#### CONCEPT 38.1

**Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle (pp. 801–811)**

- Angiosperm reproduction involves an alternation of generations between a multicellular diploid sporophyte generation and a multicellular haploid gametophyte generation. Flowers, produced by the sporophyte, function in sexual reproduction.
- The four floral organs are sepals, petals, stamens, and carpels. **Sepals** protect the floral bud. **Petals** help attract pollinators. **Stamens** bear anthers in which haploid **microspores** develop into **pollen grains** containing a male gametophyte. **Carpels** contain ovules (immature seeds) in their swollen bases. Within the ovules, **embryos sacs** (female gametophytes) develop from megasporangia.
- **Pollination**, which precedes fertilization, is the placing of pollen on the stigma of a carpel. After pollination, the pollen tube discharges two sperm into the female gametophyte. Two sperm are needed for **double fertilization**, a process in which one sperm fertilizes the egg, forming a zygote and eventually an embryo, while the other sperm combines with the polar nuclei, giving rise to food-storing endosperm.
- The **seed coat** encloses the embryo along with a food supply stocked in either the **endosperm** or the **cotyledons**. Seed **dormancy** ensures that seeds germinate only when conditions for seedling survival are optimal. The breaking of dormancy often requires environmental cues, such as temperature or lighting changes.
- The **fruit** protects the enclosed seeds and aids in wind dispersal or in the attraction of seed-dispersing animals.

**?** What changes occur to the four types of floral parts as a flower changes into a fruit?



#### CONCEPT 38.2

**Flowering plants reproduce sexually, asexually, or both (pp. 812–815)**

- **Asexual reproduction** enables successful plants to proliferate quickly. Sexual reproduction generates most of the genetic variation that makes evolutionary adaptation possible.
- Plants have evolved many mechanisms to avoid self-fertilization, including dioecy (male and female flowers on different individuals), nonsynchronous production of male and female parts within a single flower, and **self-incompatibility** reactions in which pollen grains that bear an allele identical to one in the female are rejected.
- Plants can be cloned from single cells, which can be genetically manipulated before being allowed to develop into a plant.

**?** What are the advantages and disadvantages of asexual reproduction?

#### CONCEPT 38.3

**Humans modify crops by breeding and genetic engineering (pp. 815–819)**

- Hybridization of different varieties and even species of plants is common in nature and has been used by breeders, ancient and modern, to introduce new genes into crops. After two plants are successfully hybridized, plant breeders select those progeny that have the desired traits.
- In genetic engineering, genes from unrelated organisms are incorporated into plants. Genetically modified (GM) plants have the potential of increasing the quality and quantity of food worldwide and may also become increasingly important as biofuels.
- Two important GM crops are Golden Rice, which provides more vitamin A, and *Bt* maize, which is insect resistant.
- There are concerns about the unknown risks of releasing GM organisms into the environment, but the potential benefits of transgenic crops need to be considered.

**?** Give three examples of how genetic engineering has improved food quality or agricultural productivity.

## TEST YOUR UNDERSTANDING

### LEVEL 1: KNOWLEDGE/COMPREHENSION

1. A seed develops from
  - a. an ovum.
  - b. a pollen grain.
  - c. an ovule.
  - d. an ovary.
  - e. an embryo.
2. A fruit is
  - a. a mature ovary.
  - b. a mature ovule.
  - c. a seed plus its integuments.
  - d. a fused carpel.
  - e. an enlarged embryo sac.
3. Double fertilization means that
  - a. flowers must be pollinated twice to yield fruits and seeds.
  - b. every egg must receive two sperm to produce an embryo.
  - c. one sperm is needed to fertilize the egg, and a second sperm is needed to fertilize the polar nuclei.
  - d. the egg of the embryo sac is diploid.
  - e. every sperm has two nuclei.
4. “Golden Rice”
  - a. is resistant to various herbicides, making it practical to weed rice fields with those herbicides.
  - b. is resistant to a virus that commonly attacks rice fields.
  - c. includes bacterial genes that produce a toxin that reduces damage from insect pests.
  - d. produces larger, golden grains that increase crop yields.
  - e. contains daffodil genes that increase vitamin A content.
5. Which statement concerning grafting is correct?
  - a. Stocks and scions refer to twigs of different species.
  - b. Stocks come from vines, but scions come from trees.
  - c. Stocks provide root systems for grafting.
  - d. Grafting creates new species.
  - e. Stocks and scions must come from unrelated species.

### LEVEL 2: APPLICATION/ANALYSIS

6. Some dioecious species have the XY genotype for male and XX for female. After double fertilization, what would be the genotypes of the embryos and endosperm nuclei?
  - a. embryo X/endosperm XX or embryo Y/endosperm XY
  - b. embryo XX/endosperm XX or embryo XY/endosperm XY
  - c. embryo XX/endosperm XXX or embryo XY/endosperm XYY
  - d. embryo XX/endosperm XXX or embryo XY/endosperm XXY
  - e. embryo XY/endosperm XXX or embryo XX/endosperm XYY
7. A small flower with green petals is most likely
  - a. bee-pollinated.
  - b. bird-pollinated.
  - c. bat-pollinated.
  - d. wind-pollinated.
  - e. moth-pollinated.
8. The pollen produced by wind-pollinated plants is often smaller than the pollen produced by animal-pollinated plants. A reason for this might be that
  - a. wind-pollinated plants, in general, are smaller than animal-pollinated plants.
  - b. wind-pollinated plants release pollen in the spring, before the plant has stored enough energy to make large pollen grains.
  - c. small pollen grains can be carried farther by the wind.
  - d. animal pollinators are more facile at picking up large pollen grains.
  - e. wind-pollinated flowers don’t need large pollen grains because they don’t have to attract animal pollinators.
9. The black dots that cover strawberries are actually individual fruits. The fleshy and tasty portion of a strawberry derives

from the receptacle of a flower with many separate carpels. Therefore, a strawberry is

- a. both a multiple fruit and an aggregate fruit.
- b. both a multiple fruit and an accessory fruit.
- c. both a simple fruit and an aggregate fruit.
- d. both an aggregate fruit and an accessory fruit.
- e. a simple fruit with many seeds.

10. **DRAW IT** Draw and label the parts of a flower.

### LEVEL 3: SYNTHESIS/EVALUATION

#### 11. EVOLUTION CONNECTION

With respect to sexual reproduction, some plant species are fully self-fertile, others are fully self-incompatible, and some exhibit a “mixed strategy” with partial self-incompatibility. These reproductive strategies differ in their implications for evolutionary potential. How, for example, might a self-incompatible species fare as a small founder population or remnant population in a severe population bottleneck (see Chapter 23), as compared with a self-fertile species?

#### 12. SCIENTIFIC INQUIRY

Critics of GM foods have argued that foreign genes may disturb normal cellular functioning, causing unexpected and potentially harmful substances to appear inside cells. Toxic intermediary substances that normally occur in very small amounts may arise in larger amounts, or new substances may appear. The disruption may also lead to loss of substances that help maintain normal metabolism. If you were your nation’s chief scientific advisor, how would you respond to these criticisms?

#### 13. SCIENCE, TECHNOLOGY, AND SOCIETY

Humans have engaged in genetic manipulation for millennia, producing plant and animal varieties through selective breeding and hybridization processes that significantly modify the genomes of organisms. Why do you think modern genetic engineering, which often entails introducing or modifying only one or a few genes, has met with so much public opposition? Should some forms of genetic engineering be of greater concern than others? Explain.

#### 14. WRITE ABOUT A THEME

**Emergent Properties** In a short essay (100–150 words), discuss how the ability of a flower to reproduce with other flowers of the same species is an emergent property that arises from its floral parts and their organization.

For selected answers, see Appendix A.

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