

42

Plant Reproduction

Concept Outline

42.1 Angiosperms have been incredibly successful, in part, because of their reproductive strategies.

Rise of the Flowering Plants. Animal and wind dispersal of pollen increases genetic variability in a species. Seed and fruit dispersal mechanisms allow offspring to colonize distant regions. Other features such as shortened life cycles may also have been responsible for the rapid diversification of the flowering plants.

Evolution of the Flower. A complete flower has four whorls, containing protective sepals, attractive petals, male stamens, and female ovules.

42.2 Flowering plants use animals or wind to transfer pollen between flowers.

Formation of Angiosperm Gametes. The male gametophytes are the pollen grains, and the female gametophyte is the embryo sac.

Pollination. Evolutionary modifications of flowers have enhanced effective pollination.

Self-Pollination. Self-pollination is favored in stable environments, but outcrossing enhances genetic variability.

Fertilization. Angiosperms use two sperm cells, one to fertilize the egg, the other to produce a nutrient tissue called endosperm.

42.3 Many plants can clone themselves by asexual reproduction.

Asexual Reproduction. Some plants do without sexual reproduction, instead cloning new individuals from parts of themselves.

42.4 How long do plants and plant organs live?

The Life Span of Plants. Clonal plants can live indefinitely through their propagules. Parts of plants senesce and die. Some plants reproduce sexually only once and die.



FIGURE 42.1

Reproductive success in flowering plants. Unique reproductive systems and strategies have coevolved between plants and animals, accounting for almost 250,000 flowering plants inhabiting all but the harshest environments on earth.

The remarkable evolutionary success of flowering plants can be linked to their reproductive strategies (figure 42.1). The evolution and development of flowers has been discussed in chapters 37 and 41. Here we explore reproductive strategies in the angiosperms and how their unique features, flowers and fruits, have contributed to their success. This is, in part, a story of coevolution between plants and animals that ensures greater genetic diversity by dispersing plant gametes widely. However, in a stable environment, there are advantages to maintaining the status quo genetically. Asexual reproduction is a strategy to clonally propagate individuals. An unusual twist to sexual reproduction in some flowering plants is that senescence and death of the parent plant follows.

42.1 Angiosperms have been incredibly successful, in part, because of their reproductive strategies.

Rise of the Flowering Plants

Most of the plants we see daily are angiosperms. The 250,000 species of flowering plants range in size from almost microscopic herbs to giant *Eucalyptus* trees, and their

form varies from cacti, grasses, and daisies to aquatic pondweeds. Most shrubs and trees (other than conifers and *Ginkgo*) are also in this phylum. This chapter focuses on reproduction in angiosperms (figure 42.2) because of their tremendous success and many uses by humans. Virtually all

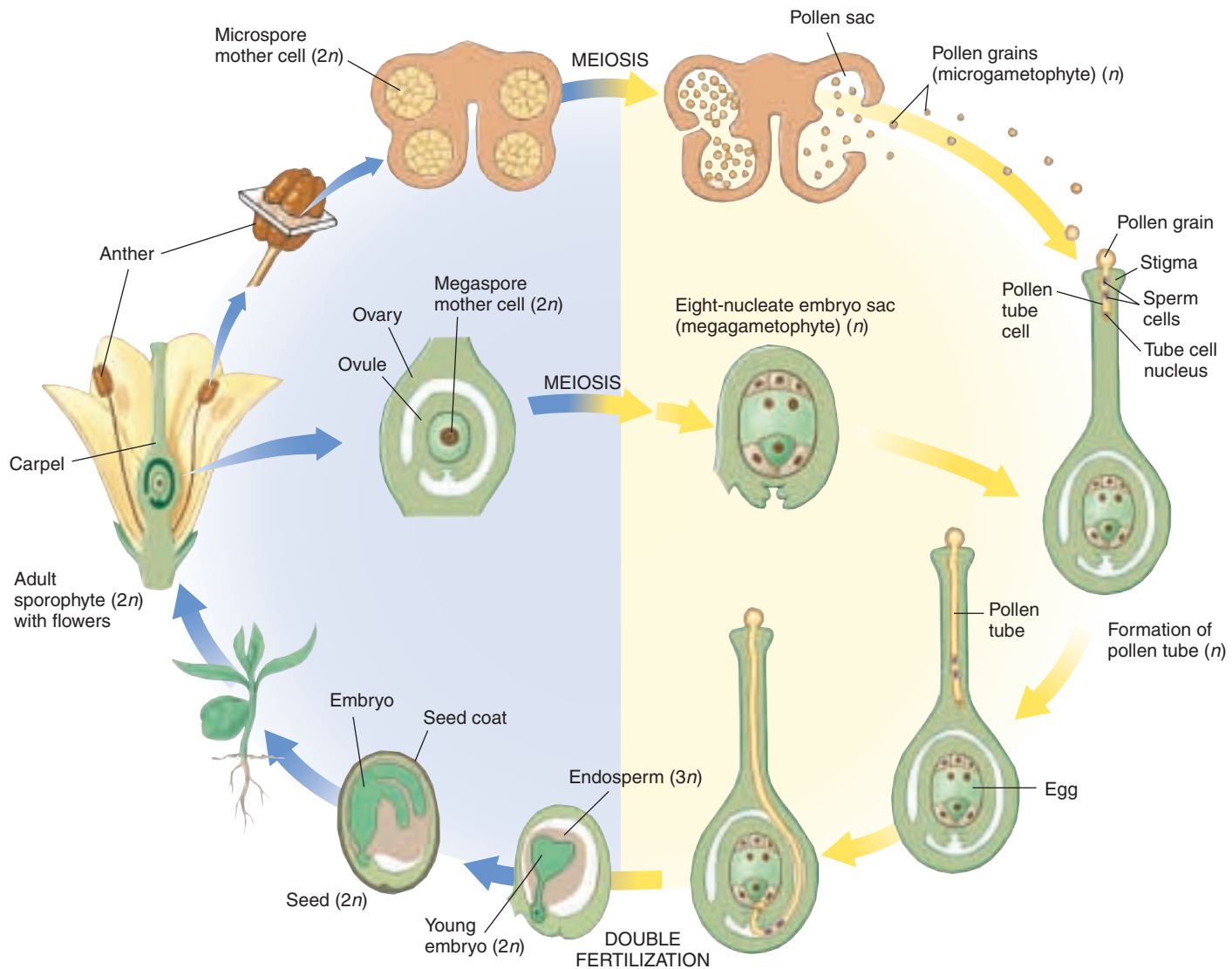


FIGURE 42.2

Angiosperm life cycle. Eggs form within the embryo sac inside the ovules, which, in turn, are enclosed in the carpels. The pollen grains, meanwhile, are formed within the sporangia of the anthers and are shed. Fertilization is a double process. A sperm and an egg come together, producing a zygote; at the same time, another sperm fuses with the polar nuclei to produce the endosperm. The endosperm is the tissue, unique to angiosperms, that nourishes the embryo and young plant.

of our food is derived, directly or indirectly, from flowering plants; in fact, more than 90% of the calories we consume come from just over 100 species. Angiosperms are also sources of medicine, clothing, and building materials. While the other plant phyla also provide resources, they are outnumbered seven to one by the angiosperms. For example, there are only about 750 extant gymnosperm species!

Why Are the Angiosperms Successful?

When flowering plants originated, Africa and South America were still connected to each other, as well as to Antarctica and India, and, via Antarctica, to Australia and New Zealand (figure 42.3). These landmasses formed the great continent known as Gondwanaland. In the north, Eurasia and North America were united, forming another supercontinent called Laurasia. The huge landmass formed by the union of South America and Africa spanned the equator and probably had a climate characterized by extreme temperatures and aridity in its interior. Similar climates occur in the interiors of major continents at present. Much of the early evolution of angiosperms may have taken place in patches of drier and less favorable habitat found in the interior of Gondwanaland. Many features of flowering plants seem to correlate with successful growth under arid and semiarid conditions.

The transfer of pollen between flowers of separate plants, sometimes over long distances, ensures *outcrossing* (cross-pollination between individuals of the same species) and may have been important in the early success of angiosperms. The various means of effective fruit dispersal that evolved in the group were also significant in the success of angiosperms (see chapter 40). The rapid life cycle of some of the angiosperms (*Arabidopsis* can go from seed to adult flowering plant in 24 days) was another factor. Asexual reproduction has given many invasive species a competitive edge. Xylem vessels and other anatomical and morphological features of the angiosperms correlate with their biological success. As early angiosperms evolved, all of these advantageous features became further elaborated and developed, and the pace of their diversification accelerated.

The Rise to Dominance

Angiosperms began to dominate temperate and tropical terrestrial communities about 80 to 90 million years ago, during the second half of the Cretaceous Period. We can document the relative abundance of different groups of plants by studying fossils that occur at the same time and place. In rocks more than 80 million years old, the fossil remains of plant phyla other than angiosperms, including lycopods, horsetails, ferns, and gymnosperms, are

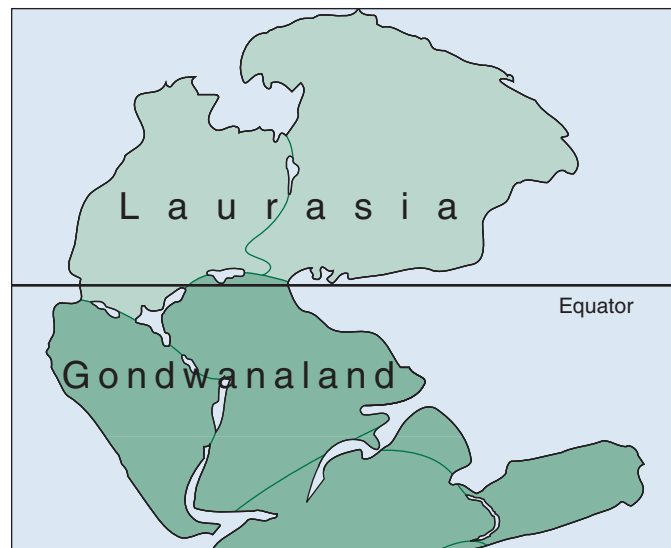


FIGURE 42.3
The alignment of the continents when the angiosperms first appeared in the fossil record about 130 million years ago. Africa, Madagascar, South America, India, Australia, and Antarctica were all connected and part of the huge continent of Gondwanaland, which eventually separated into the discrete landmasses we have today.

most common. Angiosperms arose in temperate and tropical terrestrial communities in a relatively short time.

At about the time that angiosperms became abundant in the fossil record, pollen, leaves, flowers, and fruits of some families that still survive began to appear. For example, representatives of the magnolia, beech, and legume families, which were in existence before the end of the Cretaceous Period (65 million years ago), are alive and flourishing today.

A number of insect orders that are particularly associated with flowers, such as Lepidoptera (butterflies and moths) and Diptera (flies), appeared or became more abundant during the rise of angiosperms. Plants and insects have clearly played a major role in each other's patterns of evolution, and their interactions continue to be of fundamental importance. Additional animals, including birds and mammals, now assist in pollination and seed dispersal.

By 80 to 90 million years ago, angiosperms were dominant in terrestrial habitats throughout the world.

Evolution of the Flower

Pollination in angiosperms does not involve direct contact between the pollen grain and the ovule. Pollen matures within the anthers and is transported, often by insects, birds, or other animals, to the stigma of another flower. When pollen reaches the stigma, it germinates, and a pollen tube grows down, carrying the sperm nuclei to the embryo sac. After double fertilization takes place, development of the embryo and endosperm begins. The seed matures within the ripening fruit; the germination of the seed initiates another life cycle.

Successful pollination in many angiosperms depends on the regular attraction of **pollinators** such as insects, birds, and other animals, so that pollen is transferred between plants of the same species. When animals disperse pollen, they perform the same functions for flowering plants that they do for themselves when they actively search out mates. The relationship between plant and pollinator can be quite intricate. Mutations in either partner can block reproduction. If a plant flowers at the “wrong” time, the pollinator may not be available. If the morphology of the flower or pollinator is altered, there may be physical barriers to pollination. Clearly floral morphology has coevolved with pollinators and the result is much more complex and diverse than the initiation of four distinct whorls of organs described in chapter 40.

Characteristics of Floral Evolution

The evolution of the angiosperms is a focus of chapter 37. Here we need to keep in mind that the diversity of angiosperms is partly due to the evolution of a great variety of floral phenotypes that may enhance the effectiveness of pollination. All floral organs are thought to have evolved from leaves. In early angiosperms, these organs maintain the spiral phyllotaxy often found in leaves. The trend has been toward four distinct whorls. A *complete flower* has four whorls of parts (calyx, corolla, androecium, and gynoecium), while an *incomplete flower* lacks one or more of the whorls (figure 42.4).

In both complete and incomplete flowers, the **calyx** usually constitutes the outermost whorl; it consists of flattened appendages, called **sepals**, which protect the flower in the bud. The petals collectively make up the **corolla** and may be fused. Petals function to attract pollinators. While these two outer whorls of floral organs are sterile, they can enhance reproductive success.

Androecium (from the Greek *andros*, “man,” + *oikos*, “house”) is a collective term for all the **stamens** (male structures) of a flower. Stamens are specialized structures that bear the angiosperm microsporangia. There are similar structures bearing the microsporangia in the pollen cones of gymnosperms. Most living angiosperms have stamens whose **filaments** (“stalks”) are slender and often threadlike, and whose four microsporangia are evident at

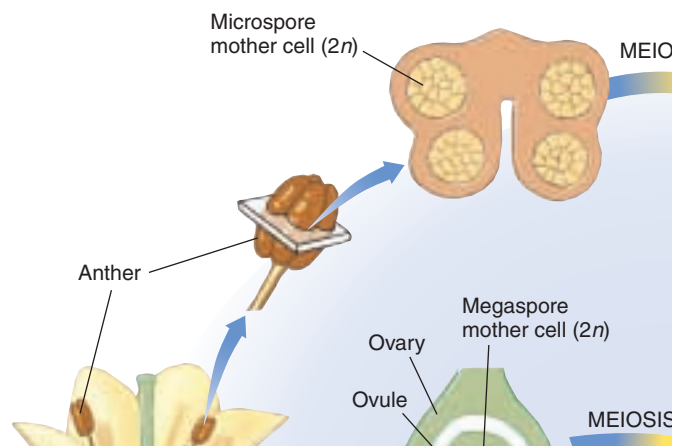


FIGURE 42.4
Structure of an angiosperm flower.

the apex in a swollen portion, the **anther**. Some of the more primitive angiosperms have stamens that are flattened and leaflike, with the sporangia producing from the upper or lower surface.

The **gynoecium** (from the Greek *gyne*, “woman,” + *oikos*, “house”) is a collective term for all the female parts of a flower. In most flowers, the gynoecium, which is unique to angiosperms, consists of a single **carpel** or two or more fused carpels. Single or fused carpels are often referred to as the simple or compound pistils, respectively. Most flowers with which we are familiar—for example, those of tomatoes and oranges—have a single compound pistil. In other mostly primitive flowers—for example, buttercups and stonecups—there may be several to many separate pistils, each formed from a single carpel. **Ovules** (which develop into seeds) are produced in the pistil’s swollen lower portion, the **ovary**, which usually narrows at the top into a slender, necklike **style** with a pollen-receptive **stigma** at its apex. Sometimes the stigma is divided, with the number of stigma branches indicating how many carpels are in the particular pistil. Carpels are essentially inrolled floral leaves with ovules along the margins. It is possible that the first carpels were leaf blades that folded longitudinally; the margins, which had hairs, did not actually fuse until the fruit developed, but the hairs interlocked and were receptive to pollen. In the course of evolution, there is evidence the hairs became localized into a stigma, a style was formed, and the fusing of the carpel margins ultimately resulted in a pistil. In many modern flowering plants, the carpels have become highly modified and are not visually distinguishable from one another unless the pistil is cut open.

Trends of Floral Specialization

Two major evolutionary trends led to the wide diversity of modern flowering plants: (1) separate floral parts have

grouped together, or fused, and (2) floral parts have been lost or reduced (figure 42.5). In the more advanced angiosperms, the number of parts in each whorl has often been reduced from many to few. The spiral patterns of attachment of all floral parts in primitive angiosperms have, in the course of evolution, given way to a single whorl at each level. The central axis of many flowers has shortened, and the whorls are close to one another. In some evolutionary lines, the members of one or more whorls have fused with one another, sometimes joining into a tube. In other kinds of flowering plants, different whorls may be fused together. Whole whorls may even be lost from the flower, which may lack sepals, petals, stamens, carpels, or various combinations of these structures. Modifications often relate to pollination mechanisms and, in some cases like the grasses, wind has replaced animals for pollen dispersal.

While much floral diversity is the result of natural selection related to pollination, it is important to recognize the impact breeding (artificial selection) has had on flower morphology. Humans have selected for practical or aesthetic traits that may have little adaptive value to species in the wild. Maize (corn), for example, has been selected to satisfy the human palate. Human intervention ensures the reproductive success of each generation; while in a natural setting modern corn would not have the same protection from herbivores as its ancestors, and the fruit dispersal mechanism would be quite different (see figure 21.13). Floral shops sell heavily bred species with modified petals, often due to polyploidy, that enhance their economic value, but not their ability to attract pollinators. In making inferences about symbioses between flowers and pollinators, be sure to look at native plants that have not been genetically altered by human intervention.

Trends in Floral Symmetry

Other trends in floral evolution have affected the symmetry of the flower (figure 42.6). Primitive flowers such as those of buttercups are *radically symmetrical*; that is, one could draw a line anywhere through the center and have two roughly equal halves. Flowers of many advanced groups are *bilaterally symmetrical*; that is, they are divisible into two equal parts along only a single plane. Examples of such flowers are snapdragons, mints, and orchids. Such bilaterally symmetrical flowers are also common among violets and peas. In these groups, they are often associated with advanced and highly precise pollination systems. Bilateral symmetry has arisen independently many times. In snapdragons, the *cyclodia* gene regulates floral symmetry, and in its absence flowers are more radial (figure 42.7). Here the evolutionary introduction of a single gene is sufficient to cause a dramatic change in morphology. Whether the same gene or functionally similar genes arose in parallel in other species is an open question.



FIGURE 42.5
Trends in floral specialization. Wild geranium, *Geranium maculatum*. The petals are reduced to five each, the stamens to ten.



FIGURE 42.6
Bilateral symmetry in an orchid. While primitive flowers are usually radially symmetrical, flowers of many advanced groups, such as the orchid family (Orchidaceae), are bilaterally symmetrical.

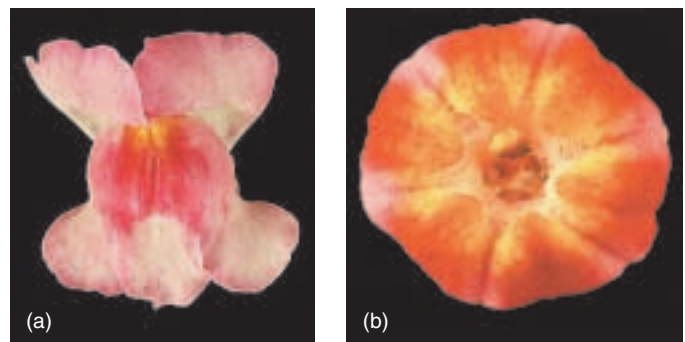


FIGURE 42.7
Genetic regulation of asymmetry in flowers. (left) Snapdragon flowers normally have bilateral symmetry. (right) The *cyclodia* gene regulates floral symmetry, and *cyclodia* mutant snapdragons have radially symmetrical flowers.

The first angiosperms likely had numerous free, spirally arranged flower parts. Modification of floral parts appears to be closely tied to pollination mechanisms. More recently, horticulturists have bred plants for aesthetic reasons resulting in an even greater diversity of flowers.

42.2 Flowering plants use animals or wind to transfer pollen between flowers.

Formation of Angiosperm Gametes

Reproductive success depends on uniting the gametes (egg and sperm) found in the embryo sacs and pollen grains of flowers. As mentioned previously, plant sexual life cycles are characterized by an alternation of generations, in which a diploid sporophyte generation gives rise to a haploid gametophyte generation. In angiosperms, the gametophyte generation is very small and is completely enclosed within the tissues of the parent sporophyte. The male gametophytes, or microgametophytes, are **pollen grains**. The female gametophyte, or megagametophyte, is the **embryo sac**. Pollen grains and the embryo sac both are produced in separate, specialized structures of the angiosperm flower.

Like animals, angiosperms have separate structures for producing male and female gametes (figure 42.8), but the reproductive organs of angiosperms are different from those of animals in two ways. First, in angiosperms, both male and female structures usually occur together in the same individual flower (with exceptions noted in chapter 38). Second, angiosperm reproductive structures are not permanent parts of the adult individual. Angiosperm flowers and reproductive organs develop seasonally, at times of the year most favorable for pollination. In some cases, reproductive structures are produced only once and the parent plant dies. It is significant that the germ line for angiosperms is not set aside early in development, but forms quite late, as detailed in chapter 40.

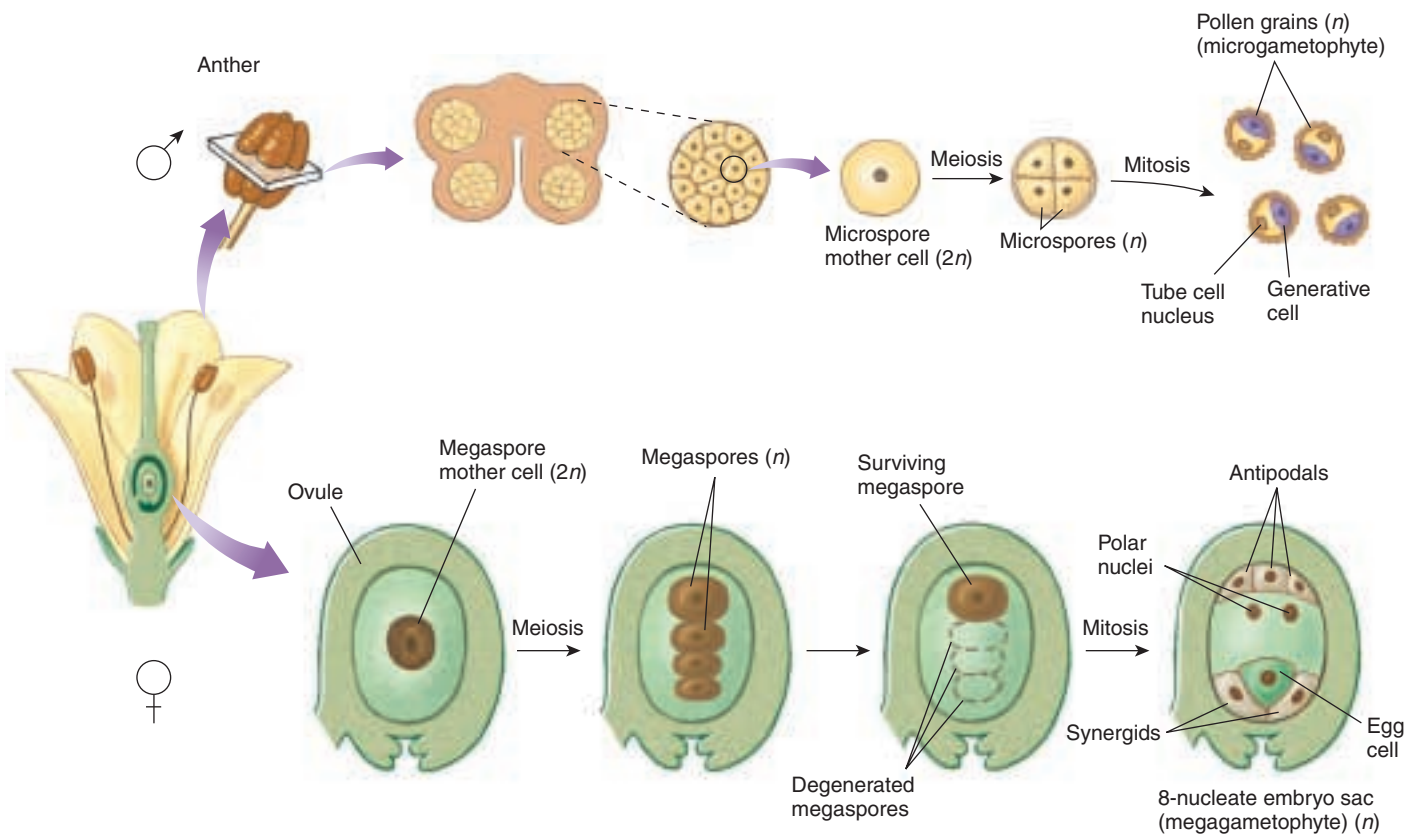
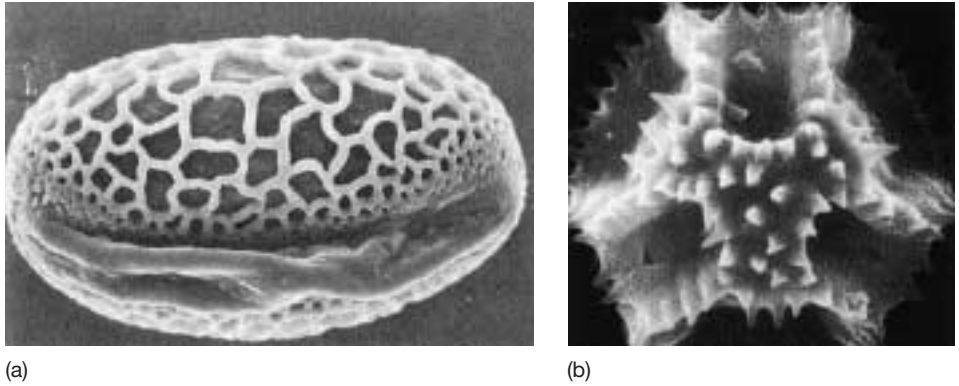


FIGURE 42.8

Formation of pollen grains and the embryo sac. Diploid ($2n$) microspore mother cells are housed in the anther and divide by meiosis to form four haploid (n) microspores. Each microspore develops by mitosis into a pollen grain. The generative cell within the pollen grain will later divide to form two sperm cells. Within the ovule, one diploid megaspore mother cell divides by meiosis to produce four haploid megaspores. Usually only one of the megaspores will survive, and the other three will degenerate. The surviving megaspore divides by mitosis to produce an embryo sac with eight nuclei.

FIGURE 42.9

Pollen grains. (a) In the Easter lily, *Lilium candidum*, the pollen tube emerges from the pollen grain through the groove or furrow that occurs on one side of the grain. (b) In a plant of the sunflower family, *Hyoseris longiloba*, three pores are hidden among the ornamentation of the pollen grain. The pollen tube may grow out through any one of them.



Pollen Formation

Pollen grains form in the two pollen sacs located in the anther. Each pollen sac contains specialized chambers in which the *microspore mother cells* are enclosed and protected. The microspore mother cells undergo meiosis to form four haploid microspores. Subsequently, mitotic divisions form four pollen grains. Inside each pollen grain is a generative cell; this cell will later divide to produce two sperm cells.

Pollen grain shapes are specialized for specific flower species. As discussed in more detail later in the chapter, fertilization requires that the pollen grain grow a tube that penetrates the style until it encounters the ovary. Most pollen grains have a furrow from which this pollen tube emerges; some grains have three furrows (figure 42.9).

Embryo Sac Formation

Eggs develop in the ovules of the angiosperm flower. Within each ovule is a megaspore mother cell. Each megaspore mother cell undergoes meiosis to produce four haploid megaspores. In most plants, only one of these megaspores, however, survives; the rest are absorbed by the ovule. The lone remaining megaspore undergoes repeated mitotic divisions to produce eight haploid nuclei that are enclosed within a seven-celled embryo sac. Within the embryo sac, the eight nuclei are arranged in precise positions. One nucleus is located near the opening of the embryo sac in the egg cell. Two are located in a single cell in the middle of the embryo sac and are called polar nuclei; two nuclei are contained in cells called synergids that flank the egg cell; and the other three nuclei reside in cells called the antipodals, located at the end of the sac, opposite the egg cell (figure 42.10). The first step in uniting the sperm in the pollen grain with the egg and polar nuclei is to get pollen germinating on the stigma of the carpel and growing toward the embryo sac.

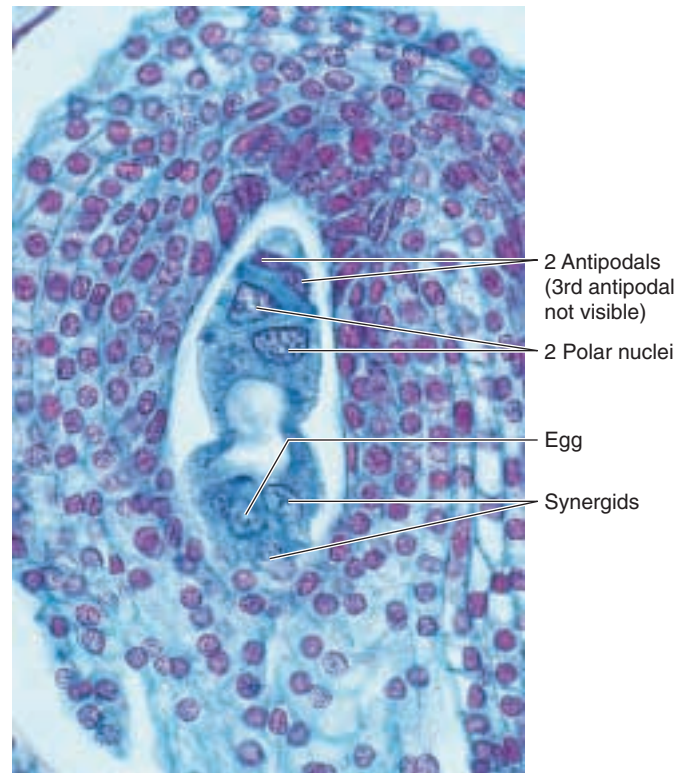


FIGURE 42.10

A mature embryo sac of a lily. The eight haploid nuclei produced by mitotic divisions of the haploid megaspore are labeled.

In angiosperms, both male and female structures often occur together in the same individual flower. These reproductive structures are not a permanent part of the adult individual and the germ line is not set aside early in development.

Pollination

Pollination is the process by which pollen is placed on the stigma. Pollen may be carried to the flower by wind or by animals, or it may originate within the individual flower itself. When pollen from a flower's anther pollinates the same flower's stigma, the process is called *self-pollination*.

Pollination in Early Seed Plants

Early seed plants were pollinated passively, by the action of the wind. As in present-day conifers, great quantities of pollen were shed and blown about, occasionally reaching the vicinity of the ovules of the same species. Individual plants of any given species must grow relatively close to one another for such a system to operate efficiently. Otherwise, the chance that any pollen will arrive at the appropriate destination is very small. The vast majority of windblown pollen travels less than 100 meters. This short distance is significant compared with the long distances pollen is routinely carried by certain insects, birds, and other animals.

Pollination by Animals

The spreading of pollen from plant to plant by pollinators visiting flowers of specific angiosperm species has played an important role in the evolutionary success of the group. It now seems clear that the earliest angiosperms, and perhaps their ancestors also, were insect-pollinated, and the coevolution of insects and plants has been important for both groups for over 100 million years. Such interactions have also been important in bringing about increased floral specialization. As flowers become increasingly specialized, so do their relationships with particular groups of insects and other animals.

Bees. Among insect-pollinated angiosperms, the most numerous groups are those pollinated by bees (figure 42.11). Like most insects, bees initially locate sources of food by odor, then orient themselves on the flower or group of flowers by its shape, color, and texture. Flowers that bees characteristically visit are often blue or yellow. Many have stripes or lines of dots that indicate the location of the nectaries, which often occur within the throats of specialized flowers. Some bees collect nectar, which is used as a source of food for adult bees and occasionally for larvae. Most of the approximately 20,000 species of bees visit flowers to obtain pollen. Pollen is used to provide food in cells where bee larvae complete their development.

Only a few hundred species of bees are social or semi-social in their nesting habits. These bees live in colonies, as do the familiar honeybee, *Apis mellifera*, and the bumble-



FIGURE 42.11
Pollination by a bumblebee. As this bumblebee, *Bombus*, squeezes into the bilaterally symmetrical, advanced flower of a member of the mint family, the stigma contacts its back and picks up any pollen that the bee may have acquired during a visit to a previous flower.

bee, *Bombus*. Such bees produce several generations a year and must shift their attention to different kinds of flowers as the season progresses. To maintain large colonies, they also must use more than one kind of flower as a food source at any given time.

Except for these social and semi-social bees and about 1000 species that are parasitic in the nests of other bees, the great majority of bees—at least 18,000 species—are solitary. Solitary bees in temperate regions characteristically have only a single generation in the course of a year. Often they are active as adults for as little as a few weeks a year.

Solitary bees often use the flowers of a given group of plants almost exclusively as sources of their larval food. The highly constant relationships of such bees with those flowers may lead to modifications, over time, in both the flowers and the bees. For example, the time of day when the flowers open may correlate with the time when the bees appear; the mouthparts of the bees may become elongated in relation to tubular flowers; or the bees' pollen-collecting apparatuses may be adapted to the pollen of the plants that they normally visit. When such relationships are established, they provide both an efficient mechanism of pollination for the flowers and a constant source of food for the bees that “specialize” on them.

Insects Other Than Bees. Among flower-visiting insects other than bees, a few groups are especially prominent. Flowers such as phlox, which are visited regularly by butterflies, often have flat “landing platforms” on which butterflies perch. They also tend to have long, slender floral tubes filled with nectar that is accessible to the long, coiled proboscis characteristic of Lepidoptera, the order of insects that includes butterflies and moths. Flowers like jimsonweed, evening primrose, and others visited regularly by moths are often white, yellow, or some other pale color; they also tend to be heavily scented, thus serving to make the flowers easy to locate at night.

Birds. Several interesting groups of plants are regularly visited and pollinated by birds, especially the hummingbirds of North and South America and the sunbirds of Africa (figure 42.12). Such plants must produce large amounts of nectar because if the birds do not find enough food to maintain themselves, they will not continue to visit flowers of that plant. Flowers producing large amounts of nectar have no advantage in being visited by insects because an insect could obtain its energy requirements at a single flower and would not cross-pollinate the flower. How are these different selective forces balanced in flowers that are “specialized” for hummingbirds and sunbirds?

Ultraviolet light is highly visible to insects. Carotenoids, yellow or orange pigments frequently found in plants, are responsible for the colors of many flowers, such as sunflowers and mustard. Carotenoids reflect both in the yellow range and in the ultraviolet range, the mixture resulting in a distinctive color called “bee’s purple.” Such yellow flowers may also be marked in distinctive ways normally invisible to us, but highly visible to bees and other insects (figure 42.13). These markings can be in the form of a bull’s-eye or a landing strip.

Red does not stand out as a distinct color to most insects, but it is a very conspicuous color to birds. To most insects, the red upper leaves of poinsettias look just like the other leaves of the plant. Consequently, even though the flowers produce abundant supplies of nectar and attract hummingbirds, insects tend to bypass them. Thus, the red color both signals to birds the presence of abundant nectar and makes that nectar as inconspicuous as possible to insects. Red is also seen again in fruits that are dispersed by birds.

Other Animals. Other animals including bats and small rodents may aid in pollination. The signals here also are species specific. These animals also assist in dispersing the seeds and fruits that result from pollination. Monkeys are attracted to orange and yellow and will be effective in dispersing those fruits.

Wind-Pollinated Angiosperms

Many angiosperms, representing a number of different groups, are wind-pollinated—a characteristic of early seed plants. Among them are such familiar plants as oaks, birches, cottonwoods, grasses, sedges, and nettles. The flowers of these plants are small, greenish, and odorless; their corollas are reduced or absent (see figures 42.14 and 42.15). Such flowers often are grouped together in fairly large numbers and may hang down in tassels that wave about in the wind and shed pollen freely. Many wind-pollinated plants have stamen- and carpel-containing flowers separated among individuals or on a single individual. If the pollen-producing and ovule-bearing flowers are separated, it is certain that pollen released to the wind will reach a flower other than the one that sheds it, a strategy



FIGURE 42.12
Hummingbirds and flowers. A long-tailed hermit hummingbird extracts nectar from the flowers of *Heliconia imbricata* in the forests of Costa Rica. Note the pollen on the bird’s beak. Hummingbirds of this group obtain nectar primarily from long, curved flowers that more or less match the length and shape of their beaks.

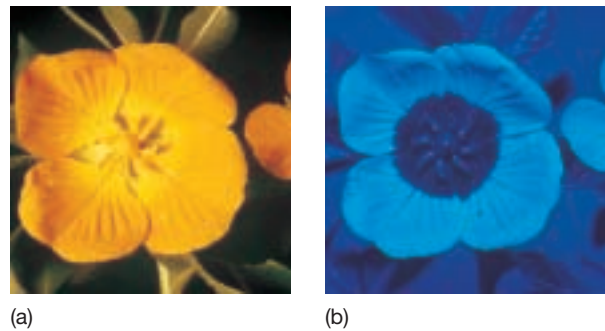


FIGURE 42.13
How a bee sees a flower. (a) The yellow flower of *Ludwigia peruviana* (Onagraceae) photographed in normal light and (b) with a filter that selectively transmits ultraviolet light. The outer sections of the petals reflect both yellow and ultraviolet, a mixture of colors called “bee’s purple”; the inner portions of the petals reflect yellow only and therefore appear dark in the photograph that emphasizes ultraviolet reflection. To a bee, this flower appears as if it has a conspicuous central bull’s-eye.

that greatly promotes outcrossing. Some wind-pollinated plants, especially trees and shrubs, flower in the spring, before the development of their leaves can interfere with the wind-borne pollen. Wind-pollinated species do not depend on the presence of a pollinator for species survival.

Bees are the most frequent and characteristic pollinators of flowers. Insects often are attracted by the odors of flowers. Bird-pollinated flowers are characteristically odorless and red, with the nectar not readily accessed by insects.

Self-Pollination

All of the modes of pollination that we have considered thus far tend to lead to outcrossing, which is as highly advantageous for plants as it is for eukaryotic organisms generally. Nevertheless, self-pollination also occurs among angiosperms, particularly in temperate regions. Most of the self-pollinating plants have small, relatively inconspicuous flowers that shed pollen directly onto the stigma, sometimes even before the bud opens. You might logically ask why there are many self-pollinated plant species if outcrossing is just as important genetically for plants as it is for animals. There are two basic reasons for the frequent occurrence of self-pollinated angiosperms:

1. Self-pollination obviously is ecologically advantageous under certain circumstances because self-pollinators do not need to be visited by animals to produce seed. As a result, self-pollinated plants expend less energy in the production of pollinator attractants and can grow in areas where the kinds of insects or other animals that might visit them are absent or very scarce—as in the Arctic or at high elevations.
2. In genetic terms, self-pollination produces progenies that are more uniform than those that result from outcrossing. Remember that because meiosis is involved, there is still recombination and the offspring will not be identical to the parent. However, such progenies may contain high proportions of individuals well-adapted to particular habitats. Self-pollination in normally outcrossing species tends to produce large numbers of ill-adapted individuals because it brings together deleterious recessive genes; but some of these combinations may be highly advantageous in particular habitats. In such habitats, it may be advantageous for the plant to continue self-pollinating indefinitely. This is the main reason many self-pollinating plant species are weeds—not only have humans made weed habitats uniform, but they have also spread the weeds all over the world.

Factors That Promote Outcrossing

Outcrossing, as we have stressed, is of critical importance for the adaptation and evolution of all eukaryotic organisms. Often flowers contain both stamens and pistils, which increase the likelihood of self-pollination. One strategy to promote outcrossing is to separate stamens and pistils.

In various species of flowering plants—for example, willows and some mulberries—staminate and pistillate flowers may occur on separate plants. Such plants, which produce only ovules or only pollen, are called **dioecious**, from the Greek words for “two houses.” Obviously, they cannot self-pollinate and must rely exclusively on outcrossing. In other kinds of plants, such as oaks, birches, corn (maize), and pumpkins, separate male and female flowers may both be produced on the same plant. Such plants are called **monoecious**,



FIGURE 42.14
Staminate and pistillate flowers of a birch, *Betula*. Birches are monoecious; their staminate flowers hang down in long, yellowish tassels, while their pistillate flowers mature into clusters of small, brownish, conelike structures.



FIGURE 42.15
Wind-pollinated flowers. The large yellow anthers, dangling on very slender filaments, are hanging out, about to shed their pollen to the wind; later, these flowers will become pistillate, with long, feathery stigmas—well suited for trapping windblown pollen—sticking far out of them. Many grasses, like this one, are therefore dichogamous.

cious, meaning “one house” (figure 42.14). In monoecious plants, the separation of pistillate and staminate flowers, which may mature at different times, greatly enhances the probability of outcrossing.

Even if, as usually is the case, functional stamens and pistils are both present in each flower of a particular plant species, these organs may reach maturity at different times. Plants in which this occurs are called **dichogamous**. If the stamens mature first, shedding their pollen before the stigmas are receptive, the flower is effectively staminate at that time. Once the stamens have finished shedding pollen, the stigma or stigmas may then become receptive, and the flower may become essentially pistillate (figures 42.15 and 42.16). This has the same effect as if the flower completely lacked either functional stamens or functional pistils; its outcrossing rate is thereby significantly increased.

Many flowers are constructed such that the stamens and stigmas do not come in contact with each other. With such an arrangement, there is a natural tendency for the pollen to be transferred to the stigma of another flower rather than to the stigma of its own flower, thereby promoting outcrossing.

Even when a flower's stamens and stigma mature at the same time, genetic **self-incompatibility**, which is widespread in flowering plants, increases outcrossing. Self-incompatibility results when the pollen and stigma recognize each other as being genetically related and fertilization is blocked (figure 42.17). Self-incompatibility is controlled by the *S* (self-incompatibility) locus. There are many alleles at the *S* locus that regulate recognition responses between the pollen and stigma. There are two types of self-incompatibility. Gametophytic self-incompatibility depends on the haploid *S* locus of the pollen and the diploid *S* locus of the stigma. If either of the *S* alleles in the stigma match the pollen *S* allele, pollen tube growth stops before it reaches the embryo sac. Petunias have gametophytic self-incompatibility. In the case of sporophytic self-incompatibility, such as in broccoli, both *S* alleles of the pollen parent are important; if the alleles in the stigma match with either of the pollen parent *S* alleles, the haploid pollen will not germinate.

Much is being learned about the cellular basis of this recognition and the signal transduction pathways that block the successful growth of the pollen tube. These pollen recognition mechanisms may have had their origins in a common ancestor of the gymnosperms. Fossils with pollen tubes from the Carboniferous are consistent



(a)



(b)

FIGURE 42.16

Dichogamy, as illustrated by the flowers of fireweed, *Epilobium angustifolium*. More than 200 years ago (in the 1790s) fireweed, which is outcrossing, was one of the first plant species to have its process of pollination described. First, the anthers shed pollen, and then the style elongates above the stamens while the four lobes of the stigma curl back and become receptive. Consequently, the flowers are functionally staminate at first, becoming pistillate about two days later. The flowers open progressively up the stem, so that the lowest are visited first. Working up the stem, the bees encounter pollen-shedding, staminate-phase flowers and become covered with pollen, which they then carry to the lower, functionally pistillate flowers of another plant. Shown here are flowers in (a) the staminate phase and (b) the pistillate phase.

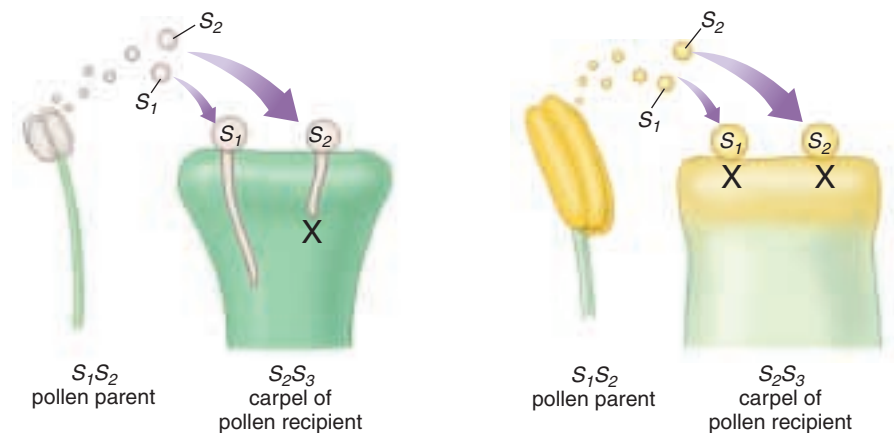
with the hypothesis that they had highly evolved pollen-recognition systems. These may have been systems that recognized foreign pollen that predated self-recognition systems.

Self-pollinated angiosperms are frequent where there is a strong selective pressure to produce large numbers of genetically uniform individuals adapted to specific, relatively uniform habitats. Outcrossing in plants may be promoted through dioecism, monoecism, self-incompatibility, or the physical separation or different maturation times of the stamens and pistils. Outcrossing promotes genetic diversity.

FIGURE 42.17

Self-pollination can be genetically controlled so self-pollen is not recognized.

(a) Gametophytic self-incompatibility is determined by the haploid pollen genotype. (b) Sporophytic self-incompatibility recognizes the genotype of the diploid pollen parent, not just the haploid pollen genotype. In both cases, the recognition is based on the *S* locus, which has many different alleles. The subscript numbers indicate the *S* allele genotype. In gametophytic self-incompatibility, the block comes after pollen tube germination. In sporophytic self-incompatibility, the pollen tube fails to germinate.



(a) Gametophytic self-incompatibility

(b) Sporophytic self-incompatibility

Fertilization

Fertilization in angiosperms is a complex, somewhat unusual process in which two sperm cells are utilized in a unique process called **double fertilization**. Double fertilization results in two key developments: (1) the fertilization of the egg, and (2) the formation of a nutrient substance called endosperm that nourishes the embryo. Once a pollen grain has been spread by wind, by animals, or through self-pollination, it adheres to the sticky, sugary substance that covers the stigma and begins to grow a **pollen tube** that pierces the style (figure 42.18). The pollen tube, nourished by the sugary substance, grows until it reaches the ovule in the ovary. Meanwhile, the generative cell within the pollen grain tube cell divides to form two sperm cells.

The pollen tube eventually reaches the embryo sac in the ovule. At the entry to the embryo sac, the tip of the pollen tube bursts and releases the two sperm cells. Simul-

taneously, the two nuclei that flank the egg cell disintegrate, and one of the sperm cells fertilizes the egg cell, forming a zygote. The other sperm cell fuses with the two polar nuclei located at the center of the embryo sac, forming the triploid ($3n$) primary endosperm nucleus. The primary endosperm nucleus eventually develops into the endosperm.

Once fertilization is complete, the embryo develops by dividing numerous times. Meanwhile, protective tissues enclose the embryo, resulting in the formation of the seed. The seed, in turn, is enclosed in another structure called the fruit. These typical angiosperm structures evolved in response to the need for seeds to be dispersed over long distances to ensure genetic variability.

In double fertilization, angiosperms utilize two sperm cells. One fertilizes the egg, while the other helps form a substance called endosperm that nourishes the embryo.

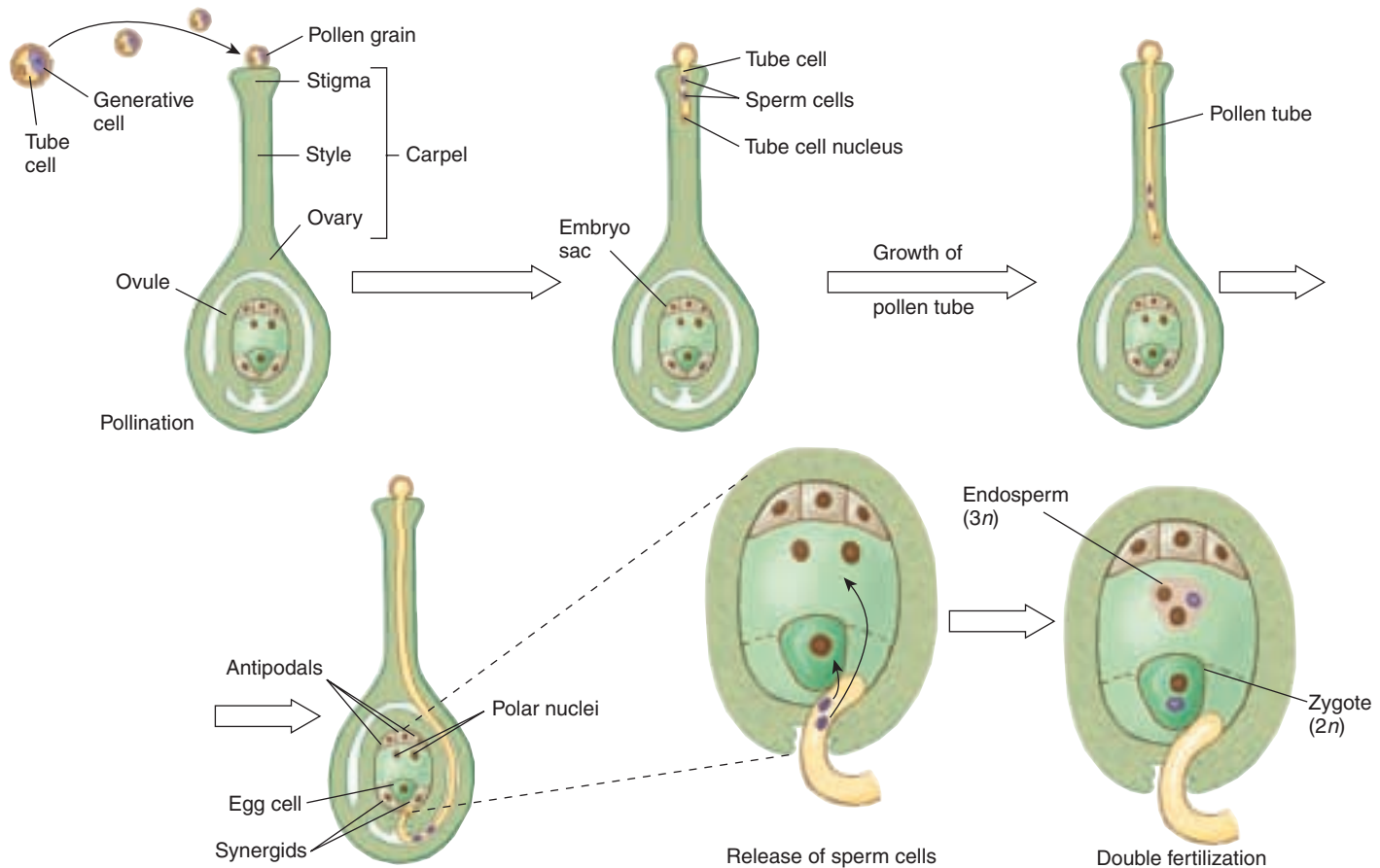


FIGURE 42.18

The formation of the pollen tube and double fertilization. When pollen lands on the stigma of a flower, the pollen tube cell grows toward the embryo sac, forming a pollen tube. While the pollen tube is growing, the generative cell divides to form two sperm cells. When the pollen tube reaches the embryo sac, it bursts through one of the synergids and releases the sperm cells. In a process called double fertilization, one sperm cell nucleus fuses with the egg cell to form the diploid ($2n$) zygote, and the other sperm cell nucleus fuses with the two polar nuclei to form the triploid ($3n$) endosperm nucleus.

42.3 Many plants can clone themselves by asexual reproduction.

Asexual Reproduction

While self-pollination reduces genetic variability, asexual reproduction results in genetically identical individuals because only mitotic cell divisions occur. In the absence of meiosis, individuals that are highly adapted to a relatively unchanging environment persist for the same reasons that self-pollination is favored. Should conditions change dramatically, there will be less variation in the population for natural selection to act upon and the species may be less likely to survive. Asexual reproduction is also used in agriculture and horticulture to propagate a particularly desirable plant whose traits would be altered by sexual reproduction, even self-pollination. Most roses and potatoes for example, are vegetatively propagated.

Vegetative Reproduction

In a very common form of asexual reproduction called vegetative reproduction, new plant individuals are simply cloned from parts of adults (figure 42.19). The forms of vegetative reproduction in plants are many and varied.

Stolons. Some plants reproduce by means of runners, or stolons—long, slender stems that grow along the surface of the soil. In the cultivated strawberry, for example, leaves, flowers, and roots are produced at every other node on the runner. Just beyond each second node, the tip of the runner turns up and becomes thickened. This thickened portion first produces adventitious roots and then a new shoot that continues the runner.

Rhizomes. Underground stems, or rhizomes, are also important reproductive structures, particularly in grasses and sedges. Rhizomes invade areas near the parent plant, and each node can give rise to a new flowering shoot. The noxious character of many weeds results from this type of growth pattern, and many garden plants, such as irises, are propagated almost entirely from rhizomes. Corms, bulbs, and tubers are rhizomes specialized for storage and reproduction. White potatoes are propagated artificially from tuber segments, each with one or more “eyes.” The eyes, or “seed pieces,” of potato give rise to the new plant.

Suckers. The roots of some plants—for example, cherry, apple, raspberry, and blackberry—produce “suckers,” or sprouts, which give rise to new plants. Commercial varieties of banana do not produce seeds and are propagated by suckers that develop from buds on underground stems. When the root of a dandelion is broken, as it may be if one attempts to pull it from the ground, each root fragment may give rise to a new plant.

Adventitious Leaves. In a few species, even the leaves are reproductive. One example is the house plant *Kalanchoë daigremontiana*



FIGURE 42.19. **Vegetative reproduction.** Small plants arise from notches along the leaves of the house plant *Kalanchoë daigremontiana*.

daigremontiana, familiar to many people as the “maternity plant,” or “mother of thousands.” The common names of this plant are based on the fact that numerous plantlets arise from meristematic tissue located in notches along the leaves. The maternity plant is ordinarily propagated by means of these small plants, which, when they mature, drop to the soil and take root.

Apomixis

In certain plants, including some citruses, certain grasses (such as Kentucky bluegrass), and dandelions, the embryos in the seeds may be produced asexually from the parent plant. This kind of asexual reproduction is known as *apomixis*. The seeds produced in this way give rise to individuals that are genetically identical to their parents. Thus, although these plants reproduce asexually by cloning diploid cells in the ovule, they also gain the advantage of seed dispersal, an adaptation usually associated with sexual reproduction. As you will see in chapter 43, embryos can also form via mitosis when plant tissues are cultured. In general, vegetative reproduction, apomixis, and other forms of asexual reproduction promote the exact reproduction of individuals that are particularly well suited to a certain environment or habitat. Asexual reproduction among plants is far more common in harsh or marginal environments, where there is little margin for variation. There is a greater proportion of asexual plants in the arctic, for example, than in temperate regions.

Plants that reproduce asexually clone new individuals from portions of the root, stem, leaves, or ovules of adult individuals. The asexually produced progeny are genetically identical to the parent individual.

42.4 How long do plants and plant organs live?

The Life Span of Plants

Plant Life Spans Vary Greatly

Once established, plants live for highly variable periods of time, depending on the species. Life span may or may not correlate with reproductive strategy. Woody plants, which have extensive secondary growth, nearly always live longer than herbaceous plants, which have limited or no secondary growth. Bristlecone pine, for example, can live upward of 4000 years. Some herbaceous plants send new stems above the ground every year, producing them from woody underground structures. Others germinate and grow, flowering just once before they die. Shorter-lived plants rarely become very woody because there is not enough time for the accumulation of secondary tissues. Depending on the length of their life cycles, herbaceous plants may be annual, biennial, or perennial, while woody plants are generally perennial (figure 42.20). Determining life span is even more complicated for clonally reproducing organisms. Aspen trees form huge clones from asexual reproduction of their roots. Collectively, an aspen clone may form the largest “organism” on earth. Other asexually reproducing plants may cover less territory but live for thousands of years. Creosote bushes in the Mojave Desert have been identified that are up to 12,000 years old!

Annual Plants

Annual plants grow, flower, and form fruits and seeds within one growing season; they then die when the process is complete. Many crop plants are annuals, including corn, wheat, and soybeans. Annuals generally grow rapidly under favorable conditions and in proportion to the availability of water or nutrients. The lateral meristems of some annuals, like sunflowers or giant ragweed, do produce poorly developed secondary tissues, but most are entirely herbaceous. Annuals typically die after flowering once, the developing flowers or embryos using hormonal signaling to reallocate nutrients so the parent plant literally starves to death. This can be demonstrated by comparing a population of bean plants where the beans are continually picked with a population where the beans are left on the plant. The frequently picked population will continue to grow and yield beans much longer than the untouched population. The process that leads to the death of a plant is called *senescence*.



FIGURE 42.20
Annual and perennial plants. Plants live for very different lengths of time. (a) Desert annuals complete their entire life span in a few weeks. (b) Some trees, such as the giant redwood (*Sequoiadendron giganteum*), which occurs in scattered groves along the western slopes of the Sierra Nevada in California, live 2000 years or more.

Biennial Plants

Biennial plants, which are much less common than annuals, have life cycles that take two years to complete. During the first year, biennials store photosynthate in underground storage organs. During the second year of growth, flowering stems are produced using energy stored in the underground parts of the plant. Certain crop plants, including carrots, cabbage, and beets, are biennials, but these plants generally are harvested for food during their first season, before they flower. They are grown for their leaves or roots, not for their fruits or seeds. Wild biennials include evening primroses, Queen Anne’s lace, and mullein. Many plants that are considered biennials actually do not flower until they are three or more years of age, but all biennial plants flower only once before they die.

Perennial Plants

Perennial plants continue to grow year after year and may be herbaceous, as are many woodland, wetland, and prairie wildflowers, or woody, as are trees and shrubs. The majority of vascular plant species are perennials. Herbaceous perennials rarely experience any secondary growth in their stems; the stems die each year after a period of relatively rapid growth and food accumulation. Food is often stored in the plants’ roots or underground stems, which can become quite large in comparison to their less substantial aboveground counterparts.

Trees and shrubs generally flower repeatedly, but there are exceptions. Bamboo lives for many seasons as a vegetative plant, but senescens and dies after flowering.

Chapter 42Chapter