37 Reproduction in Flowering Plants

Dr. Jeremy Burgess/Science Photo Library/Photo Researchers, Inc.

Flower of the common chickweed. This plant (*Stellaria media*) is a weedy annual native to Europe but widespread in North America. Each flower has five green sepals, five deeply notched yellow petals, three to five pollen-bearing stamens (this flower has three), and a single pistil.

KEY CONCEPTS

37.1 The flower is the site of sexual reproduction in angiosperms. A typical flower consists of four whorls: sepals, petals, stamens, and carpels.

37.2 Pollen grains are transported to stigmas by a variety of agents, such as animals and wind.

37.3 Double fertilization results in a plant embryo and endosperm. The seed is a mature ovule, and the fruit is a mature ovary.

37.4 Following a period of dormancy, a seed germinates, or sprouts. The young seedling becomes anchored in the ground and begins to photosynthesize.

37.5 Many vegetative organs (roots, stems, and leaves) are modified for asexual reproduction.

37.6 Sexual reproduction in flowers results in genetic variability in the offspring, whereas asexual reproduction in vegetative structures generally results in individuals that are genetically identical.

Flowering plants, or **angiosperms,** include about 300,000 species and are the largest, most successful group of plants. You may have admired flowers for their fragrances as well as their appealing colors and varied shapes (see photograph). The biological function of flowers is sexual reproduction. Their colors, shapes, and fragrances increase the likelihood that pollen grains, which produce sperm cells, will be carried from one plant to another. Sexual reproduction in plants includes *meiosis* and the fusion of reproductive cells—egg and sperm cells, collectively called **gametes.** The union of gametes, called fertilization, occurs within the flower's ovary.

Sexual reproduction offers the advantage of new gene combinations, not found in either parent, that may make an individual plant better suited to its environment. These new combinations result from the crossing-over and independent assortment of chromosomes that occur during meiosis, before the production of egg and sperm cells (see Chapter 11).

Many flowering plants also reproduce asexually. Asexual reproduction often does not involve the formation of flowers, seeds, and fruits. Instead, offspring generally form when a vegetative organ (such as a stem, root, or leaf) expands, grows, and then becomes separated from the rest of the plant, often by the death of tissues. Because asexual reproduction requires only one parent and no meiosis or fusion of gametes occurs, the offspring of asexual reproduction are virtually genetically identical to one another and to the parent plant.[1]

This chapter examines both sexual and asexual reproduction in flowering plants, including floral adaptations that are important in pollination; seed and fruit structure and dispersal; germination and early growth; and several kinds of asexual reproduction. We conclude with a discussion of the evolutionary advantages and disadvantages of sexual and asexual reproduction.

37.1 THE FLOWERING PLANT LIFE CYCLE

LEARNING OBJECTIVES

1 Describe the functions of each part of a flower.
2 Identify where eggs and pollen grains are formed within the flower.

In Chapters 27 and 28 you learned that angiosperms and other plants undergo a cyclic **alternation of generations** in which they spend a portion of their life cycle in a multicellular haploid stage and a portion in a multicellular diploid stage. The haploid portion, called the **gametophyte generation,** gives rise to gametes by mitosis. When two gametes fuse during **fertilization,** the diploid portion of the life cycle, called the **sporophyte generation,** begins. The sporophyte generation produces haploid spores by meiosis. Each spore has the potential to give rise to a gametophyte plant, and the cycle continues.

In flowering plants the diploid sporophyte generation is larger and nutritionally independent. The haploid gametophyte generation, which is located in the flower, is microscopic and nutritionally dependent on the sporophyte. We say more about alternation of generations in flowering plants after our discussion of the role of flowers as reproductive structures. (It may be helpful for you to review Figure 28-13, which shows the main stages in the flowering plant life cycle.)

Flowers develop at apical meristems

How does a plant "know" it is time to start forming flowers? Correct timing in the switch from vegetative to reproductive development is crucial to ensure reproductive success. A variety of environmental cues, such as temperature and day length, ensure proper timing, and different species are adapted to respond to distinct environmental cues. These environmental signals interact with a variety of plant hormones and developmental pathways.

In recent years some biologists have focused on the molecular aspects of developmental pathways that initiate flowering in plants such as the model organism *Arabidopsis.* When environmental conditions induce flowering, many genes are activated or inactivated. One gene, the *Flowering Locus C (FLC)* gene, codes for a **transcription factor** that represses flowering. Another gene, called *Flowering Locus D (FLD)* gene, codes for a protein that removes acetyl groups from histones in the chromatin where the *FLC* gene is located. When deacetylation occurs, the *FLC* gene is not transcribed (that is, the repressive transcription factor is not produced), and the shoot apical meristem undergoes a transition from vegetative growth to reproductive growth. It is intriguing that the plant FLD protein is homologous to a mammalian protein that also removes acetyl groups from chromatin.

Other genes are also involved in the initiation of flowering, and this area remains a focus of active research interest. In Chapter 38 we discuss the initiation of flowering further.

Each part of a flower has a specific function

Flowers are reproductive shoots, usually consisting of four kinds of organs—sepals, petals, stamens, and carpels—arranged in whorls (circles) on the end of a flower stalk (**FIG. 37-1**; also see Fig. 28-11). In flowers with all four organs, the normal order of whorls from the flower's periphery to the center (or from the flower's base upward) is as follows:

sepals ⟶ petals ⟶ stamens ⟶ carpels

The tip of the stalk enlarges to form a **receptacle** on which some or all of the flower parts are borne. All four floral parts are important in the reproductive process, but only the stamens (the "male" organs) and carpels (the "female" organs) participate directly in sexual reproduction—sepals and petals are sterile.

Sepals, which constitute the outermost and lowest whorl on a floral shoot, cover and protect the flower parts when the flower is a bud. Sepals are leaflike in shape and form and are often green. Some sepals, such as those in lily flowers, are colored and resemble petals (**FIG. 37-2**). The collective term for all the sepals of a flower is **calyx.**

The whorl just inside and above the sepals consists of **petals,** which are broad, flat, and thin (like sepals and leaves) but widely varied in shape and frequently brightly colored, which attracts pollinators. Petals play an important role in ensuring that sexual reproduction will occur. Sometimes petals fuse to form a tube or other floral shape. The collective term for all the petals of a flower is **corolla.**

Just inside and above the petals are the **stamens,** the male reproductive organs. Each stamen has a thin stalk, called a **filament,** at the top of which is an **anther,** a saclike structure in which **pollen grains** form. For sexual reproduction to occur, pollen grains must be transferred from the anther to the female reproductive structure (the carpel), usually of another flower of the same species. At first, each pollen grain consists of two cells surrounded by a tough outer wall. One cell, the **generative cell,** divides mitotically to form two nonflagellate male gametes, known as *sperm cells.* The other cell, the **tube cell,** produces a **pollen tube,** through which the sperm cells travel to reach the ovule.

One or more **carpels,** the female reproductive organs, are located in the center or top of most flowers. Carpels bear **ovules,**

[1]Somatic mutations can result in some variability among asexually derived offspring.

which are structures with the potential to develop into seeds. The carpels of a flower may be separate or fused into a single structure. The female part of the flower, often called a **pistil,** may be a single carpel (a *simple pistil*) or a group of fused carpels (a *compound pistil*) (see Fig. 28-12). Each pistil has three sections: a **stigma,** on which the pollen grains land; a **style,** a necklike structure through which the pollen tube grows; and an **ovary,** a juglike structure that contains one or more ovules and can develop into a fruit.

Considerable variation in flower structure occurs from one species to another, but flower structure is virtually constant within a given species. For that reason, flower structure is important in plant identification and, if flowers are present, flowering plant species are easy to evaluate in the field.

Female gametophytes are produced in the ovary, male gametophytes in the anther

Before we proceed, it may be helpful to relate the stages in alternation of generations to floral structure. As discussed in Chapters 27 and 28, angiosperms and certain other plants are heterosporous and produce two kinds of spores: megaspores and microspores (**FIG. 37-3**).

Each young ovule within an ovary contains a diploid cell, the *megasporocyte,* which undergoes meiosis to produce four haploid **megaspores.** Three of these usually disintegrate, and the fourth, the functional megaspore, divides mitotically to produce a multicellular **female gametophyte,** also called an *embryo sac.* The female gametophyte, which is embedded in the ovule, typically contains seven cells with eight haploid nuclei. Six of these cells, including the egg cell (the female gamete), contain a single nucleus each; a large central cell has two nuclei, called **polar nuclei.** The egg and both polar nuclei participate directly in fertilization.

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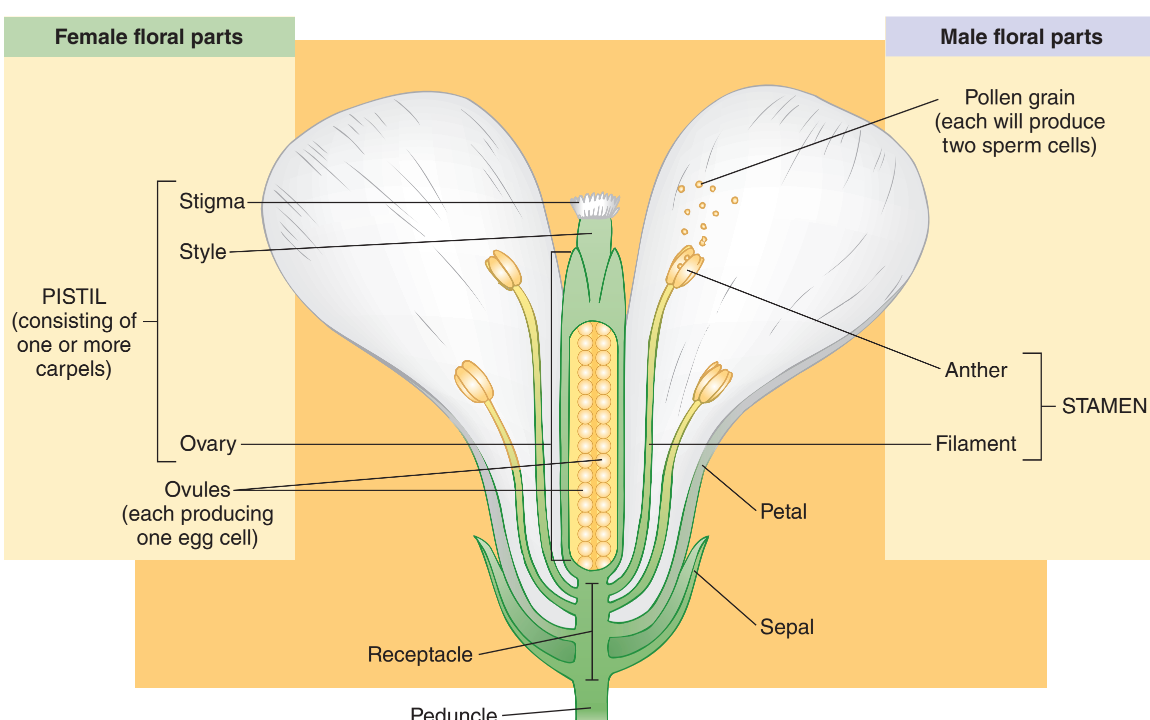
(a) An *Arabidopsis thaliana* flower.



(b) Cutaway view of an *Arabidopsis* flower. Each flower has four sepals (*two are shown*), four petals (*two are shown*), six stamens, and one long pistil. Four of the stamens are long, and two are short (*two long and two short are shown*). Pollen grains develop within sacs in the anthers. In *Arabidopsis*, the compound pistil consists of two carpels that each contain numerous ovules.

FIGURE 37-1 ***Animated*** **Floral structure**

FIGURE 37-2 Lily flowers
In lily (*Lilium*) the three sepals and three petals are similar in size and color.

Pollen sacs within the anther contain numerous diploid cells called *microsporocytes,* each of which undergoes meiosis to produce four haploid cells called **microspores.** Each microspore divides mitotically to produce an immature male gametophyte, also called a pollen grain, that consists of two cells, the tube cell and the generative cell. The pollen grain becomes mature when its generative cell divides to form two nonmotile sperm cells.

Review

- How do petals differ from sepals? How are they similar?
- How do stamens differ from carpels? How are they similar?
- What are female gametophytes, and where are they formed?
- What are male gametophytes, and where are they formed?

37.2 POLLINATION

LEARNING OBJECTIVES

3. Compare the evolutionary adaptations that characterize flowers pollinated in different ways (by insects, birds, and bats).
4. Define *coevolution* and give examples of ways that plants and their animal pollinators have affected one another's evolution.

Before fertilization can occur, pollen grains must travel from the anther (where they form) to the stigma. The transfer of pollen grains from anther to stigma is known as **pollination.** Plants are *self-pollinated* if pollination occurs within the same flower or a different flower on the same individual plant. When pollen grains are transferred to a flower on another individual of the same species, the plant is *cross-pollinated.* Flowering plants accomplish pollination in a variety of ways. Beetles, bees, flies, butterflies, moths, wasps, and other insects pollinate many flowers. Animals such as birds, bats, snails, and small nonflying mammals (rodents, primates, and marsupials) also pollinate plants. Wind is an agent of pollination for certain flowers; and water, for a few aquatic flowers.

Many plants have mechanisms that prevent self-pollination

In plant sexual reproduction, the two gametes that unite to form a zygote may be from the same parent or from two different parents. The combination of gametes from two different parents increases the variation in offspring, and this variation may confer a selective advantage. Some offspring, for example, may be able to survive environmental changes better than either parent can.

Evolution has resulted in a variety of mechanisms that prevent self-pollination and thus prevent **inbreeding,** which is the mating of genetically similar individuals. Inbreeding can increase the concentration of harmful genes in the offspring. Some plants, such as asparagus and willow, have separate male and female individuals; the male plants have staminate flowers that lack carpels, and the female plants have pistillate flowers that lack stamens. Other species have flowers with both stamens and pistils, but the pollen is shed from a given flower either before or after the time when the stigma of that flower is receptive to pollen. These characteristics promote **outcrossing** (also called outbreeding), which is the mating of dissimilar individuals.

Many species have genes for **self-incompatibility,** a genetic condition in which the pollen is ineffective in fertilizing the same flower or other flowers on the same plant. In other words, an individual plant can identify and reject its own pollen. Genes for self-incompatibility usually inhibit the growth of the pollen tube in the stigma and style, thereby preventing delivery of sperm cells to the ovules. Self-incompatibility, which is more common in wild species than in cultivated plants, ensures that reproduction occurs only if the pollen comes from a genetically different individual.

In plants such as oilseed rape, self-incompatibility is based on a high degree of variation at a particular locus called the *S* locus; the many alleles at this locus are designated S_1, S_2, S_3, S_4, and so on. Here is an example of how the *S* locus blocks self-fertilization: A plant with the genotype S_1S_2 produces pollen grains that land on a stigma of another plant with the genotype S_1S_3. In this case, the presence of the S_1 allele in both the pollen and stigma triggers a self-recognition signaling cascade in surface cells of the stigma. As a result, the stigma cells do not undergo changes that allow the pollen grain to grow a pollen tube. Therefore, fertilization does not occur.

The molecular basis of self-incompatibility in *Arabidopsis* and related plants is an area of active scientific interest. *Arabidopsis* can self-pollinate. Biologists have determined that the genes involved in self-incompatibility and outcrossing exist in *Arabidopsis* but have undergone mutations so that they are no longer functional. Thus, it appears that self-incompatibility in these plants is the ancestral (normal) condition.

Flowering plants and their animal pollinators have coevolved

Animal pollinators and the plants they pollinate have had such close, interdependent relationships over time that they have affected the evolution of certain physical and behavioral features in one another. The term **coevolution** describes such reciprocal adaptation, in which two species interact so closely that they become increasingly adapted to each other as they each undergo evo-

KEY POINT In alternation of generations in flowering plants, the female and male gametophytes are microscopic and nutritionally dependent on the sporophyte plant.

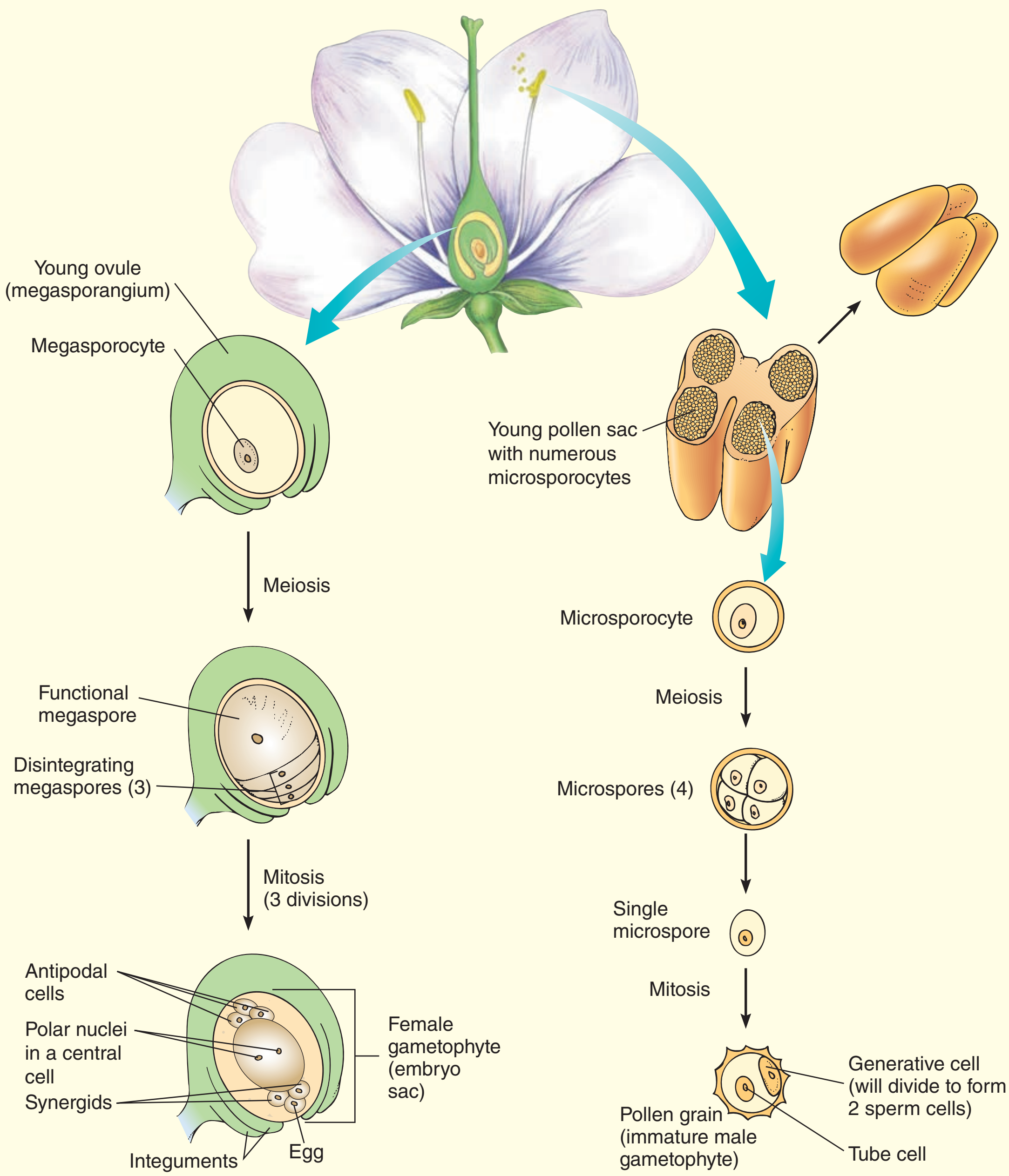


FIGURE 37-3 *Animated* **Development of female and male gametophytes**
(*Left side*) The female gametophyte, or embryo sac, develops within the ovule. (*Right side*) The immature male gametophytes, or pollen grains, develop within pollen sacs in the anthers.

lutionary change by *natural selection*. We now examine some of the features of flowers and their pollinators that may be the products of coevolution.

Flowers pollinated by animals have various features to attract their pollinators, including showy petals (a visual attractant) and scent (an olfactory attractant) (**FIG. 37-4** and **TABLE 37-1**). One reward for the animal pollinator is food. Pollen grains are a protein-rich food for many animals. As they move from flower to flower searching for food, pollinators inadvertently carry along pollen grains on their body parts, helping the plants reproduce sexually.