

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 increases 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



FIGURE 42.14
Staminate and pistillate flowers of a birch, *Betula* sp. 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.

monoecious, 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 pollen tube growth 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 molecular and biochemical 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 Carbonifer-



(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.

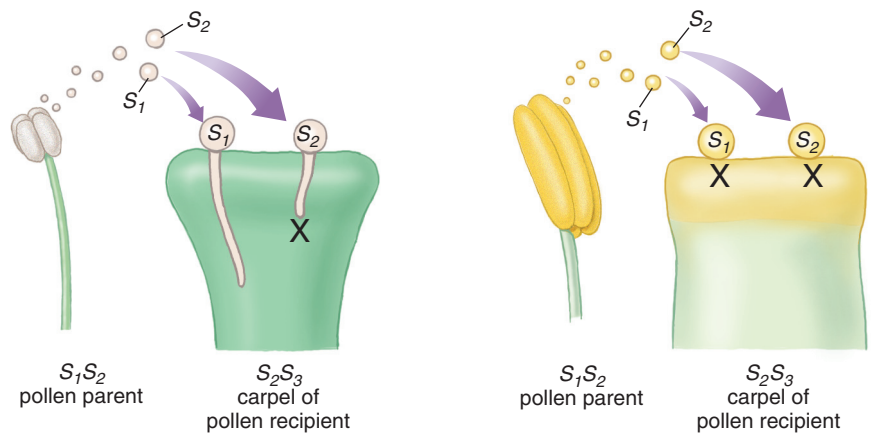
ous Period are consistent with the hypothesis that they had highly evolved pollen-recognition systems. These may have been systems that recognized foreign pollen that predated self-recognition systems.

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 blocked.

(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