

PLANT REPRODUCTIVE SYSTEMS

Plants have reproductive systems that are more variable than those in most animals. In many plants, both sexual and asexual means of reproduction are possible. The combination of both means of reproduction can be highly advantageous for plants, especially for perennials. When sexual reproduction is prevented or averted, either by physical damage to the plants or by unfavorable environmental conditions, perennials usually can persist vegetatively until conditions are favorable for sexual reproduction. The main advantage of sexual reproduction is that it provides an opportunity for organisms to produce new combinations of genes or to pass on to succeeding generations new mutations that might be highly adaptive to changing environments or to other conditions. Recombination occurs through the reassortment of parental genes during meiosis and subsequent combination of those genes during fertilization.

The reproductive organs for angiosperms are the flowers. Most plants have bisexual flowers with all four floral parts (sepals, petals, stamens, and carpels) present. If only one of the sexual parts (stamens or carpels) is present, the flower is unisexual. The sepals and petals constitute the perianth and are accessory in that they are not directly involved with the sexual life cycle. The perianth functions in protecting the stamens and carpels, the sexual parts, and in attracting animal pollinators to the flower. The stamens and carpels are the essential parts of a flower because they produce the gametes for sexual reproduction.

Pollination, or the transfer of pollen to an appropriate stigma, is an integral part of the sexual life cycle of flowering plants. Pollinators, typically insects, birds, or bats, first need to be attracted to a flower and then provided an enticement to return or to go to another flower of the same species. Generally, animals are attracted to a flower by an odor or by the color and shape of the corolla. Odors may be barely evident, sweet, musky, or fetid. Floral shapes show numerous variations that may either inhibit or promote visitations from particular animal pollinators. For example, a large beetle is able to move freely on an open, dish-shaped flower (e.g., *Magnolia*), but is unable to get inside a flower that has a narrow tubular base (e.g., *Phlox*). Corolla shapes vary from open and dish-shaped to tubular. Floral types that influence how pollen is placed on an animal visitor (pollinator) include: a brush flower (e.g., willows or burnet) in which the perianth is reduced and the reproductive parts are prominent; a flag flower (e.g. lupine or sweetpea) in which there is a banner, two wings, and a keel (housing the reproductive parts); and a gullet flower (e.g., snapdragon or *Penstemon*) in which the lower lip serves as a landing platform and the upper lip encloses or is closest to the reproductive parts. The rewards that flowers offer animal visitors are pollen, nectar, and special food bodies usually consisting of fats and oils. In some cases, animal visitors may be able to chew holes in the corolla or manipulate the floral parts to extract the rewards without pollinating the flower.

By noting the structure, odor, and color of flowers, one can reasonably predict a probable pollinator. **Beetles** tend to visit and pollinate flowers that are actinomorphic, dull-colored, musky, without nectar guides, and with plenty of pollen and possibly

special food bodies. **Flies** visit two types of flowers. The carrion flies visit usually maroon or green flowers that lack nectar guides and that have a rotten, fetid odor. The small flies may visit open, dish-shaped flowers that are light blue or yellow, with faint nectar guides, and with no or faint odor. **Bees** are rather indiscriminate, but prefer flowers that are blue or yellow and with moderately abundant nectar. **Butterflies** usually visit tubular flowers with vivid colors and with plenty of nectar. **Moths** typically visit tubular, white flowers that open at night or at dusk; these usually have strong and sweet odors and abundant nectar, but lack nectar guides. **Bats** visit bell-shaped or tubular flowers that open at night or at dusk; the flowers may be white, maroonish or a drab color and have strong odors reminiscent of fermentation. **Hummingbirds** prefer red, tubular flowers that produce abundant nectar; these flowers generally lack an odor and are erect or at right angles to the stem axis. **Wind-pollinated** flowers typically have a reduced or inconspicuous perianth, large stamens that produce abundant, smooth pollen, and a gynoecium with an enlarged stigmatic area; adaptations for wind pollination appear to set the stage in many groups for the development of unisexual flowers from bisexual ones.

Plants that reproduce sexually may do so either by **inbreeding** or **outbreeding**. Inbreeding refers to a condition where the plants are genetically self-compatible and often self-pollinating; in some cases, cross-pollination may occur so long as it is between genetically similar individuals. When plants are 'crossed', pollen is transferred from the anther of a flower on one plant to a receptive stigma in a flower on a different plant. **Selfing** typically involves the transfer of pollen from anther to receptive stigma within a given flower (with or without the aid of animal vectors), or it may include a condition known as **geitonogamy** in which pollen is transferred (usually by animals) between flowers on the same plant. Outbreeding plants are genetically different and cross-pollinated. They may be either self-compatible or self-incompatible. If self-compatible, the outbreeders generally have evolved floral mechanisms to prevent selfing. If the plants are self-incompatible, pollen will not germinate on the stigma or grow through the style of a flower on the plant in which the pollen is produced.

Self-compatible plants that are self-pollinating are termed **autogamous**. Flowers of autogamous plants tend to be small, have monocolored sepals and petals, lack nectar guides or nectaries and have stamens and carpels maturing simultaneously. The number of pollen grains and ovules produced is less than in outcrossing plants. Autogamous plants are good colonizers and often occur in the first stages of ecological succession. They usually have a broad geographic distribution and may be known as weeds. Seed-set is assured and most, if not all, of the fruits on a given plant will form seed. A population of autogamous individuals or inbreeders will tend to be very similar morphologically, with not nearly as much variation as is evident in outbreeding populations. Taxonomically, several isolated inbreeding populations are difficult to analyze because each is internally homogeneous but noticeably different between populations; they form a collection of morphological 'islands' difficult to group together as a species. Occasionally, plants that are typical inbreeders will outcross. This capability will diversify the genetic make-up and may lead to an altered breeding system of the species.

The ultimate in autogamy is found in those self-compatible, inbreeding flowers that never open, yet produce seed by sexual means. This condition ensures seed set and is known as **cleistogamy**. In some species of *Viola* (family Violaceae), cleistogamous flowers are produced either at the beginning or at the end of the flowering season, while showy outcrossing flowers occur throughout most of the flowering period.

Various methods of outcrossing have developed in flowering plants. The most efficient system involves genetically self-incompatible flowers. Many outcrossers, however, are genetically self-compatible and, in these, floral modifications have evolved that enhance cross-pollination. Outcrossers tend to have showy perianths, nectar guides and nectaries (if animal-pollinated), a large amount of pollen and numerous ovules, and reproductive structures that mature at different times. Because of chance pollination events, only some of the fruits mature and only a portion of the ovules ripen into seeds.

Floral mechanisms that tend to prevent selfing in an outcrossing plant are varied. In some plants, particularly milkweeds and orchids, the male and female structures are physically separated within the flower. **Temporal isolation** between the reproductive parts of flowers occurs when one sexual part matures before the other. **Protandry** occurs when stamens mature and release pollen before stigmas in the same flower are receptive. When stigmas become receptive before stamens mature in the same flower, the condition is termed **protogyny**. Generally, plants that form unisexual flowers tend to be outcrossers. There are two basic conditions when unisexuality prevails, one in which male (staminate) and female (carpellate or pistillate) flowers occur on the same plant (**monoecious** condition) and the other in which the male and female flowers occur on different plants (**dioecious** condition). Generally, the flowers of dioecious plants are small, and white, yellow, or pale green. Dioecism is more common in plants with a woody habit than in those with a herbaceous habit. The costs of dioecism are high because only the female or carpellate plants produce seeds. The advantages of insured outbreeding tend to offset the disadvantages of dioecism. In some instances, the two sexes of dioecious species specialize to slightly different microhabitats, which might enhance pollinator success or permit escape from certain seed predators. Once plants have evolved dioecism, there is usually little change in the way they reproduce. It appears to be an irreversible reproductive system.

Asexual reproduction, often called **apomixis**, involves the formation of genetically identical individuals. When these occur together, the group is called a **clone**. Either vegetative or reproductive organs may produce propagules or plant parts that serve to reproduce replicates of an individual. Stems reproduce asexually by the production of runners (stolons), bulbs, or bulblets, or by the terminal part of a stem bending over and rooting in the soil (layering). Leaves may be rooted or, in some cases, form small fragments that serve as asexual propagules. Less commonly, asexual seeds are formed by circumventing fertilization in the ovules. In these cases of agamospermy (meaning seeds formed without gametes), a diploid cell within an ovule divides by mitosis to produce cells that form an asexual embryo while other cells of the ovule form an integument around the developing embryo.