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Pollination

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The transport of pollen grains from the plant parts that produce them to the ovule-bearing organs, or to the ovules (seed precursors) themselves. In gymnosperms (plants with naked seeds), including conifers and cycads, the pollen, usually dispersed by the wind, is simply caught by a drop of fluid excreted by each freely exposed ovule. In angiosperms (flowering plants), where the ovules are contained in the pistil, the pollen is deposited on the pistil's receptive end (the stigma), where it germinates. *See also:* Flower (/content/flower/261900); Palynology (/content/palynology/484800); Pollen (/content/pollen/533100); Seed (/content/seed/612600); Seed germination (/content/seed-germination/900110)

Ideally, each pollen grain forms a pollen tube, which grows down through the slender style (stalk of the pistil) toward one of the ovules enclosed in the basal part or ovary. Here, one of the two sperm cells within the pollen tube fuses with the egg cell of the ovule, making possible the development of an embryo, whereas the other sperm cell combines with two so-called polar nuclei of the ovule, thus starting the formation of endosperm, a tissue rich in reserve food. After this double fertilization, the ovule enlarges and becomes transformed into a seed.

Without pollination, there would be no fertilization; thus it is of crucial importance for the production of fruit crops and seed crops. Pollination also plays an important part in plant-breeding experiments that are aimed at increasing crop production through the creation of genetically superior types. *See also:* <u>Agricultural science (plant) (/content/agricultural-science-plant/015900)</u>; <u>Breeding (plant) (/content/breeding-plant/095100)</u>; <u>Fertilization (plant) (/content/fertilization-plant/802970)</u>; <u>Plant reproduction (/content/plant-reproduction/581300)</u></u>

Self- and cross-pollination

In most plants, self-pollination is difficult or impossible, and there are various mechanisms that are responsible. For example, in dichogamous flowers, the pistils and stamens reach maturity at different times; in protogyny, the pistils mature first; and in protandry, the stamens mature before the pistils. Selfing is also impossible in dioecious species, such as date palms and willows, where some plants bear flowers that have only pistils (pistillate or female flowers), whereas other individuals have flowers that produce only pollen (staminate or male flowers). In monoecious species, such as hazel, where pistillate and staminate flowers are found on the same plant, self-breeding is at least reduced. Heterostyly, as exemplified by certain primroses, is another device that promotes outbreeding. Here, some flowers (pins) possess a long pistil and short stamens, while others (thrums) exhibit the reverse condition; each plant individual bears only pins or only thrums. Pollen transport from stamens to pistils of the same length is easy; however, in the other cases, it is difficult.

Flower attractants

As immobile organisms, plants normally need external agents for pollen transport. These can be insects, wind, birds, mammals, or water, roughly in that order of importance. In some plants, for example, certain arum lilies, Dutchman's-pipes, and orchids, the pollinators are simply trapped. In the large majority of cases, though, the flowers offer one or more rewards, such as sugary nectar, oil, solid food bodies, perfume, sex, an opportunity to breed (as in figs), a place to sleep (*Serapias* orchids), or some of the pollen itself. For the attraction of pollinators, flowers provide either visual or olfactory signals. Color includes ultraviolet, which is perceived as a color by most insects and at least some hummingbird species. Fragrance is characteristic of flowers that are pollinated by bees, butterflies, or hawkmoths, whereas carrion or dung odors are produced by flowers that cater to certain beetles and flies. By using a combination of olfactory and visual signals, a few orchids (including *Ophrys* and *Cryptostylis* species) mimic females of certain bees or wasps so successfully that the corresponding male insects will try to mate with them, thus achieving pollination (pseudocopulation).

At close range, pollinating insects are guided to the nectar in many cases by special color patterns, lines, or dots, known as nectar or honey guides. Olfactory honey guides and osmophores (particular flower parts specialized for odor production) may be equally important. For better evaporation of odors, a number of flowers also may develop considerable heat through a special process known as thermogenic respiration (this occurs in certain arum lilies and water lilies).

Animal pollinators

Although some flowers are generalists, catering to a whole array of different animals, others (such as *Ophrys*) are highly specialized, being pollinated by only a single species of insect. Extreme pollinator specificity is an important factor in maintaining the purity of plant species in the field, even in those cases where hybridization can easily be achieved artificially in a greenhouse or laboratory, as in most orchids. The almost incredible mutual adaptation between pollinating animal and flower that can frequently be observed exemplifies the idea of coevolution. *See also:* **Plant-animal interactions (/content /plant-animal-interactions/757349)**

Bird pollination

Hummingbirds have good red vision and feed on the wing. Flowers pollinated by these birds are often orange and red and they hang down freely or are exposed (*Fuchsia*); they are sturdy, lack a landing platform, are open in the daytime, have little or no odor, and offer a not-too-concentrated nectar. Plants with flowers pollinated by birds other than hummingbirds (such as sunbirds in Africa) usually provide perches. *See also:* **Apodiformes (/content/apodiformes/043800)**

Bat pollination

Flowers pollinated by bats include those of the sausage tree, saguaro cactus, cup-and-saucer vine, and certain bananas. They are open in the evening, when they emit a rank or musty odor; their petal colors are either murky and nondescript or snow white; they are wide-mouthed and often bell-shaped; and they normally offer both nectar and pollen in abundance. In connection with the poorly developed sonar sense of pollinating bats, these flowers often hang down freely from ropelike twigs (flagelliflory) or are on the main stem or limbs of the tree (cauliflory). These phenomena, however, may also be connected with the dispersal, by bats, of the fruits and seeds, even though the pollinators may have been different animals. *See also:* Chiroptera (/content/chiroptera/130600)

Hawkmoth pollination

Flowers pollinated by hawkmoths have a great deal in common with those pollinated by hummingbirds, but they are white or light-colored and very fragrant, especially in the evening when they are open.

Butterfly pollination

Flowers pollinated by butterflies open in the daytime, are usually colorful and fragrant [butterfly bush (*Buddleia*) and lilacs], and either offer a flat landing space (*Impatiens*) or, when small, are combined in inflorescences that provide flattish surfaces to be walked on (red valerian and *Buddleia*). The narrow flower tubes allow entry of the slender butterfly proboscis, but discriminate against other insects. *See also:* Lepidoptera (/content/lepidoptera/377700)

Fly and beetle pollination

Both flies and beetles are highly diversified groups, making it difficult to describe "typical" fly- or beetle-pollinated flowers. Trap flowers exploit types such as carrion and dung beetles (or flies), which are not at all adapted to flowers. However, many modern flowers cater to animals with highly specialized mouthparts, such as certain longhorn beetles and the bee-fly *Bombylius. See also:* <u>Coleoptera (/content/coleoptera/148200);</u> <u>Diptera (/content/diptera/198700)</u>

Bee pollination

By far, the most important of all insect pollinators are the social bees, especially honeybees (*Apis*) and bumblebees (*Bombus*). Whereas the former are subtropical in origin, bumblebees are adapted to cold climates. The larvae of both *Apis* and *Bombus* live on pollen and honey (a modified nectar); the adults drink nectar.

Among the physical and behavioral adaptations that the adults possess to obtain these foods are long tongues, hairy bodies, special pollen baskets on the hindlegs, and a good color sense. The four broad color regions that are distinguished by bees are yellow, blue-green, blue, and ultraviolet. The bees learn very quickly to associate colors or minty odors with food, and they remember the link for several weeks. These traits, and the bees' excellent time sense, which enables them to visit flowers when these have the most to offer, are important in the establishment of flower constancy: the bees stay with one, or very few, crop plants only, which is important for seed production.

Honeybees can distinguish various sugars. In contrast to bumblebees, which are rugged individualists, honeybees have an excellent communication system: a worker bee can indicate both the direction and the distance of a rich food source by means of special dances, so that the resource can be exploited cooperatively. Flowers pollinated by bees, for example, true sage, bleeding heart, and Scotch broom, generally have bright colors, minty odors, and a landing platform; in addition, they often display bilateral symmetry. Their pollen grains are sticky, spiny, or highly sculptured for better adherence to the bees. *See also:* Beekeeping (/content/beekeeping/076800); Hymenoptera (/content/hymenoptera/331700); Social insects (/content/social-insects/630700)

Wind pollination

Wind pollination is prevalent in the primitive cycads and in conifers, but it is also found in such familiar flowering plants as grasses, rushes, sedges, cattails, plantains, nettles, hemp, sorrel, lamb's-quarters, alder, birch, hazel, poplars, and temperate-region oaks. It offers advantages in regions where animal pollinators are scarce or where these cannot operate as a result of adverse environmental or seasonal conditions, such as strong winds. Wind-pollinated flowers are usually inconspicuous, being devoid of attractants and rewards for pollinators. They lack showy petals, fragrance, and nectar.

To facilitate exposure to the wind, blooming often takes place in early spring before the leaves have emerged, or the flowers may be placed very high on the plant. In a number of species, the anthers burst open in an explosive fashion, scattering the pollen widely; the stigmas often are long and divided into arms or lobes, or they are feathery (like those of some willows and cereals), thereby facilitating pollen catching. The latter process is also promoted because, in open areas, wind-pollinated plants of one species often grow together in dense populations. The pollen grains, which are shed singly, are dry, lack glue, and are smooth-surfaced; in some cases (for example, pine and cedar), they are provided with air sacs. Wind pollination,

however, is a wasteful process because it lacks precision. For example, although one male plant of *Mercurialis annua*, a common weed, may produce 1.25×10^9 pollen grains, there is only a slim chance that an individual stigma will be hit by more than one or two pollen grains. Undoubtedly in connection with this, the number of ovules per pistil and (later) the number of seeds per fruit is very low (two ovules per flower in beech, hazel, oak, and walnut; one per flower in birch, grasses, elm, stinging nettle, and sweet gale).

Water pollination

Although the pollen grains of some plants can be made to germinate in aqueous sugar solutions, water alone in most cases will destroy them. Accordingly, water is seldom the true medium of pollen dispersal, even in aquatic plants. In ribbon weed (*Vallisneria*), the male and female flowers are released to the surface separately. At the surface, male flowers are driven by the wind until they bump into female flowers; the shock causes the pollen to be catapulted over to the stigma. True water dispersal of pollen (hydrophily), in which the grains are wetted, is found only in the freshwater hornworts (*Ceratophyllum*) and marine eelgrasses (*Zostera* and *Phyllospadix*).

Ecology

Traditionally, pollination biology has considered mechanisms that promote or guarantee the proper transfer of pollen from one individual of a given plant species to another. Often this involves a careful description of the transfer mechanism coupled to a particular pollinating agent (such as hawkmoths, bumblebees, bats, or wind). Pollinator-plant interactions, however, have also been used as a model for understanding broader evolutionary and ecological issues that pertain to all living systems. Pollination systems have proven to be an excellent model for studying many current issues in population biology.

Since plants have a variety of breeding structures, they provide an opportunity for assessing the reproductive value of different sexual strategies and for modeling the evolution of breeding systems and sexual allocation. A classic problem in animal populations is the number of males and females that a mother should produce as offspring (the sex ratio). Hypotheses that account for the evolution of the sex ratio can be tested by using dioecious plant species, and speculations on sex-ratio evolution can be far more complicated in plants as a result of their striking variety in methods of sexual allocation (such as gynodioecy, androdioecy, or hermaphroditism).

If pollen movement is considered as a measurable analog of gene movement, then pollination systems are ideal for unraveling patterns of gene flow and the concomitant genetic structuring of plant populations. Pollen transfer can be measured by numerous methods. Gene flow (or the lack of it) has been implicated in retarding (or promoting) local population adaptation to different habitats, as well as affecting rates of species formation. The traditional and the ecological approaches to pollination studies are distinguishable by their different views on the important consequences of pollen transfer. The traditional view stresses the mechanism of transfer within individual flowers or plants, whereas the ecological view stresses the population consequences of transfer among many individuals, even across communities or habitats. *See also:* **Population ecology (/content/population-ecology/538150)**; **Population genetics (/content/population-genetics/538200)**

Pollinators are often faced with having to make complicated decisions about when, where, and what flowers to forage. Therefore they have been used as models for testing hypotheses that are concerned with animal behavior, such as patterns of learning, the acquisition of information from the environment, or alteration of behavior associated with changes in the environment.

The complex interaction among plants and their pollinators has prompted research on community-level ecology as well as on population-level approaches. The timing of flowering within given habitats may reflect competitive interactions among plants for pollination, and competition may also affect the kinds of pollinators that are found in a habitat and their pattern of resource

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use. The evolutionary ecology of many plants and pollinators may be best understood as a result of complex interactions among populations of many species. *See also:* <u>Ecological communities (/content/ecological-communities/212130);</u> Ecological competition (/content/ecological-competition/757554); Ecology (/content/ecology/212500); Population dispersal (/content/population-dispersal/537900)

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