Chapter Three

Plant Reproductive Biology

Higher plants have alternation of generations, with a gametophyte generation being reduced to the status of a short-lived parasite on the sporophyte generation. What most of us think of as a "plant" and its flowers are actually parts of the diploid, sporophytic generation (Figure 3.1). Most of the flower itself consists of evolutionarily specialized structures of the sporophyte.

However, hidden within the ovary of the flower, specialized cells undergo meiosis to create the haploid megaspore mother cells. The megaspore divides three times to produce the embryo sac, which is the female gametophyte and will produce female gametes, eggs (Figure 3.1). Meanwhile, inside the anthers other cells under go meiosis to produce haploid microspores. Microspores also undergo mitosis to produce pollen grains, which are the male gametophyte. The single celled pollen grain has two nuclei. When a pollen grain is transferred to the stigma (part of the sporophyte), one of the nuclei divides to produce two sperm nuclei, which are the male gametes. The pollen grain itself "germinates" to grow a long tube down the stigma and style to the ovary. Here one of the sperm nuclei fuses with an egg to produce a diploid zygote, which divides mitotically many times to produce an embryo. The other sperm nucleus fuses with other nuclei in the ovule to produce the triploid endosperm, which acts as food for the embryo and germinating seedling. The two fusions of nuclei are referred to, appropriately enough, as "double fertilization."

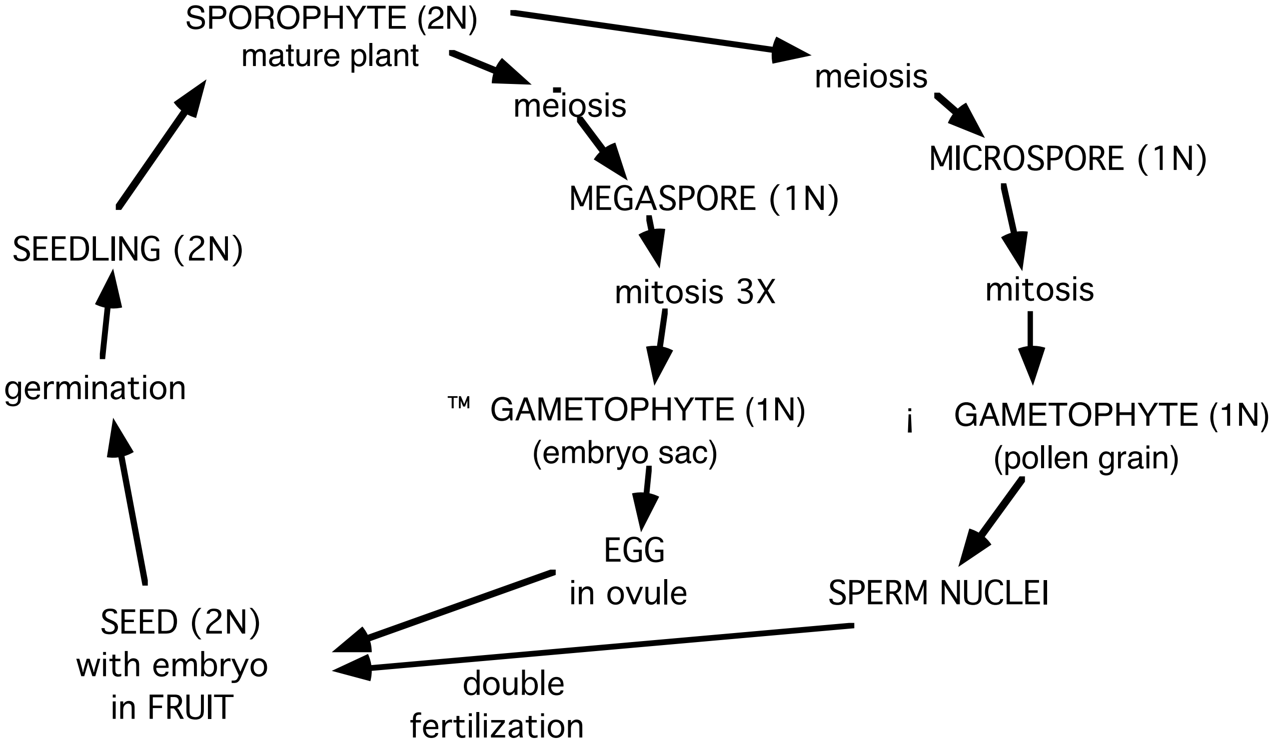

Figure 3.1. Alternation of generations in the life cycle of higher plants. Note that the haploid sexual generations (gametophytes) are substantially reduced and dependent upon the diploid asexual generation (sporophytes).

Outcrossing and Selfing

In order for pollination to occur, pollen grains must travel from the “male” structures (the anthers) of the flower where they are produced to the “female” structure (the stigma) where pollen is received. The majority of higher plant species are hermaphroditic, meaning that a single individual produces both male and female gametes. This means that unlike many more familiar organisms (like mammals), a single individual may sometimes be both the father and the mother of its offspring. When pollen from a plant fertilizes ovules of the same individual, we refer to the process as **self-pollination**, or **selfing**. When pollen from one plant fertilizes ovules of a genetically distinct individual, the process is called **outcrossing**.

Self-pollination can be a perfectly acceptable means of reproduction for some plant species. In fact, some species, such as the premier model organism in plant genetics, *Arabidopsis thaliana*, rely almost exclusively on selfing. Selfing can occur through pollination of an ovule by pollen from the same flower, which is called autogamy. Pollination between different flowers is called allogamy. Allogamy that occurs when pollen is carried from one flower to another on the same plant is called geitonogamy. True outcrossing, in which pollen is carried from a flower on one plant to a flower on a different plant is called xenogamy.

Although selfing is acceptable and even desirable for some species, for other species, selfing is undesirable because it results in **inbreeding depression**, or reduced fitness of offspring derived from matings among related individuals relative to offspring produced by unrelated individuals. Although plants cannot move, and therefore must rely on forces outside of their immediate control to move pollen from anthers to stigmas, they have evolved a variety of means of influencing whether they are selfed or outcrossed.

Most species are either predominantly self-pollinating or predominantly outcrossing, not intermediate in strategy (Schemske and Lande, 1985). Selfing, where it exists, appears to be a secondarily derived condition. That is, ancestors of these species were outcrossing and then evolved self-pollination. As evidence, many plants produce colorful flowers, lots of nectar and pollen, and attract significant numbers of pollinators, yet are entirely selfing and require no pollination. It is clear that, in these cases, ancestral species that required outcrossing were involved in the evolution of the flower.

Evolution by natural selection has apparently acted to promote outcrossing in many ways. These are all very important to keep in mind when looking at any given flower, because much of its structure is likely to be the result of past selection for allogamy. Let's consider some of the most common ways in which plants prevent pollination from occurring within an individual.

Separation in Space

The simplest way for plants to prevent autogamous self-fertilization is to separate the anthers physically from the stigma. In flowers that are hermaphroditic (i.e. those that produce both male and female gametes), this separation virtually always occurs. When the bud opens, the two structures will physically separate themselves before the pollen is released and the stigma becomes receptive. Having flowers that contain both male and female parts separated in space is termed herkogamy.

Extreme examples of herkogamy can be found in orchids and milkweeds (Asclepiadaceae, butterfly weed is a good example). In both these groups, all the pollen is packed into fairly hard masses with a wax-like appearance, called pollinia (singular, pollinium). These pollinia are usually located in a kind of "key" mechanism in the flower so that they are only removed from the flower when the pollinator is leaving and only deposited onto the next flower when the pollinator arrives. It is very difficult for them to be deposited in the flower of origin.

Of course, herkogamous flowers are still susceptible to transfer of pollen within a flower by pollinators, or even by the wind or other disturbances. A more effective arrangement is actually to have separate male and female flowers. Monoecious species have both male and female flowers on the same plant. In this case, autogamy is impossible, yet the genetically equivalent geitonogamy is still likely, as pollinators frequently move between flowers on the same plant (Table 3.1). Some species avoid this problem by only having a small number of flowers open at a time.

Dioecious species actually have plants of different "sex." Recognize that we are using a convenient short-hand: the sporophyte plants themselves are sexless but produce gametophytes which are male or female. Although dioecy enforces xenogamy, it does so at the expense of half the population not bearing seeds and creates a risk of nonpollination (Table 3.1). For example, species that persist by colonizing new habitats are not likely to be dioecious, as both a male and a female plant would have to be lucky enough to colonize a new area at the same time.

An interesting way in which the male and female function can be separated in plants is a form of heteromorphy (literally, different shapes), distyly and tristyly. Heteromorphy is simply the condition in which some individuals in the population have a structure different from that of others, and in this case it has to do with the relative locations of the stigma and anthers in different flowers (Figure 3.2). For example, in distyly, there are two forms of the plant. One produces flowers in which the stigma is located high in the flower and the stamens somewhat lower, and the other produces the opposite arrangement, the stigma low and the stamens high. This strategy discourages pollination within a flower and encourages pollen transfer between flowers. In our area, heterostyly occurs in many species, including several Oxalis species and species in the coffee family, as well as in purple loosestrife (Lythrum salicaria) and pickerel weed (Pontederia cordata). Charles Darwin was one of the first to recognize the significance of the different locations of stamens and pistils in his wonderful book The Different Forms of Flowers on Plants of the same Species.

Separation in Time

We define anthesis as beginning when the anthers or the stigmas become exposed to the pollinating agent(s), either because the flower opens or because the organs protrude from a closed flower in such a manner as to expose themselves to the same agent. When pollen grains are fully mature, the anthers often split open and begin to shed the pollen. When the stigma is mature and can accept pollen, we say it is receptive. The stigma may not be continuously receptive during anthesis and, in fact, self-pollination can be prevented by careful timing of stigma receptivity relative to pollen maturation within the same flower.

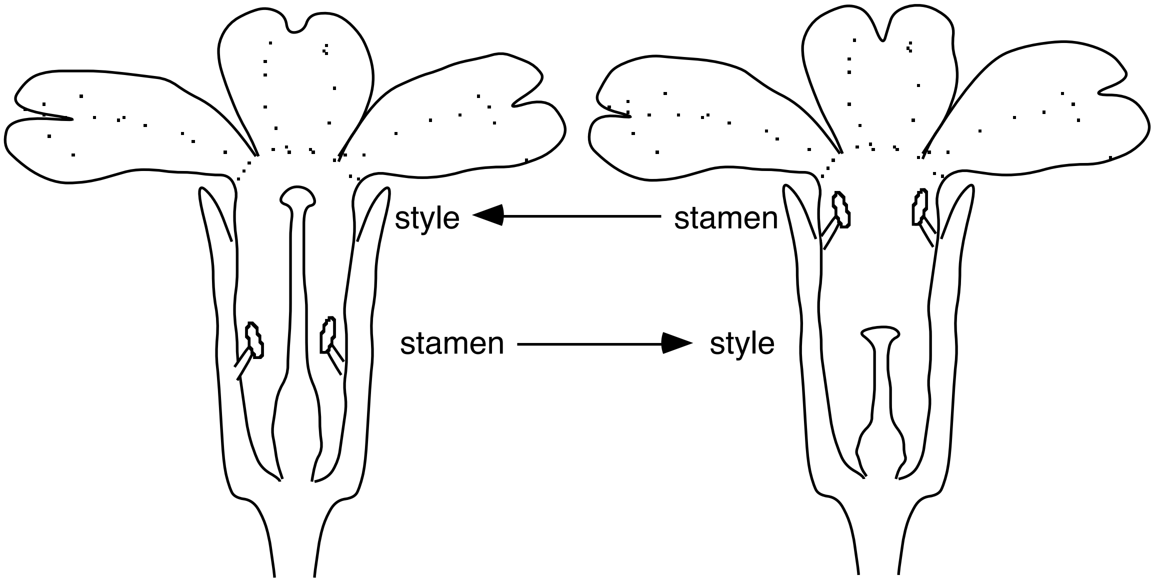

Figure 3.2. Distyly in Primula. Note the two different types of flowers, one having long styles and stamens low in the floral tube, the other having short styles and stamens near the mouth of the tube. Long-styled flowers are only receptive to pollen transported from the anthers of short-styled flowers and vice versa.

Dichogamy describes the case in which the stamens and pistil of a flower mature at different times, thereby preventing autogamous self-pollination. There are two types of dichogamy: Protandry, in which the anthers mature and release pollen before the stigmas are receptive, and protogyny, in which the stigmas become receptive before pollen release. Protandry is found in most composites (Asteraceae) and also in many mints (Lamiaceae) and figworts (Scrophulariaceae). In both cases, the temporal separation of the sexes enforces allogamy, can encourage xenogamy, and can allow each sexual function to occur at a time that may be more advantageous to the plant (Table 3.1).

Good examples of protandry are often provided by species with columnar or spike inflorescences, such as the bumblebee-pollinated foxgloves (Digitalis purpurea) and fireweed (Epilobium angustifolium). Both the opening of the flower buds and the production of nectar in the flowers follow a very strict time pattern, geared to the foraging strategy of the pollinators. The inflorescences of these plants bloom from the bottom up, and each flower lasts several days. Therefore the lowest flowers on an inflorescence with many open flowers are female, having gone through the male stage already. These flowers are also the richest in nectar, and foraging bumblebees nearly always visit them first, with the result that any pollen deposited on their stigmas is likely to have come from another plant. The bumblebees then work their way up the inflorescence, visiting several flowers in succession until the nectar reward is no longer commensurate with the energy they have to expend in order to get it. They then fly off, usually to the lowest flowers of another inflorescence, where the pollen they have picked up from the higher-placed flowers may be deposited on the stigma. The result is usually cross-pollination.

Protogyny is very pronounced in a number of families commonly regarded as primitive, for example, water lilies (Nymphaeaceae) and magnolias (Magnoliaceae). Very common plants that demonstrate protogyny are the plantains (Plantaginaceae). These species have flowers arranged on spikes and flower from the bottom up, just as do foxglove and fireweed. However, in these species older flowers are male rather than female. Therefore, in an inflorescence with many open flowers, it is the bottom ones that are male, whereas those higher up are female. Because plantains depend on the wind for pollination, the likelihood of pollen traveling upwards is very low, and the situation favors cross-pollination.

Autogamy and Apomixis

Many species do not avoid autogamy. In some flowers, self-pollination is spontaneous, so that even if no external pollination agent (biotic or abiotic) touches the flower, its own structures cause the transfer of pollen from anthers to stigma. The evolution of such pollination methods is thought to be a "retrograde" development; that is, that it has evolved from outcrossing ancestors, perhaps as compensation for poor chances for allogamous pollination.

Weedy species present special problems with regard to allogamy. It has even been suggested that autogamy is a prerequisite for the successful establishment of long distance migrants, perhaps because long-distance dispersal isolates plants from their normal pollinators. Evolutionarily, there are two options: (1) a generalized flower form that attracts many different types of pollinators and/or (2) autogamy.

Another mechanism to insure fertilization found in weedy species is apomixis--the development of a sporophyte from a gametophyte without fertilization, the equivalent of parthenogenesis in animals. In this case, there is no self- or outcrossed fertilization. Apomixy can occur in several ways. In many apomictic species, the megaspore mother cell goes through meiosis to produce the egg, but the egg chromosome number at some time simply doubles. In other species, there is no meiosis at all; the so-called "egg" is produced by mitosis and already has the diploid chromosome number. Clearly, apomictic species do not require pollination.

Now, if a flower is already pollinated before it opens, and there is no likelihood of later pollination having any effect, the whole anthesis is functionally redundant, and could be done away with. Cleistogamous (from two Greek words together meaning a secret marriage) flowers never open and have a marked reduction (or elimination) in portions of the flower affecting advertisement and pollinator rewards. Generally, the anthers and number of pollen grains are also reduced in accord with the greater efficiency of this pollination process.

Cleistogamous species are distributed worldwide: well-known examples include violets, rushes, wood sorrel, and some rice species. Practically all cleistogamous plants can also produce normal open or chasmogamous flowers. Cleistogamy appears to be related to environmental conditions: when the environment is harsh, plants are more likely to produce cleistogamous flowers. The classic example is jewel weed (Impatiens capensis), an annual species that in moist, high-light environments produces many large and beautiful chasmogamous flowers, which offer large amounts of nectar to pollinating bees. However, on unfavorable sites, the plants are stunted and produce only cleistogamous flowers. The main advantage of cleistogamy is that it is a cheap method. Producing and maintaining large, nectar-rich open flowers is biologically expensive. The cost of producing a seed through cleistogamy is only about two-thirds of that for one formed through chasmogamy. Another interesting point is that well-developed jewel weed plants that would normally form a number of chasmogamous flowers will make only cleistogamous ones after they have been grazed by deer or when the ends of the branches have been cut off--a quick response to an emergency situation.

Self-Incompatibility

Separation of male and female flower parts in time and space are prepollination mechanisms to reduce selfing. That is, they act to reduce the probability that self-pollination will occur. There are also postpollination mechanisms of reducing selfing. An example is self-incompatibility. In a self-incompatible species, self pollen that reaches a stigma does not produce viable seed. Self-incompatibility often supplements other mechanisms promoting outcrossing, so a species may demonstrate herkogamy and also be self-incompatible. Self-incompatibility is not invariably absolute; in fact, it varies from 100% to a very slight advantage for foreign pollen. Incompatibility is a prerequisite for allogamous pollination in many flowers in which pollen and receptive stigma inevitably come into contact with each other (i.e. in which there is no herkogamy).

Incompatibility can take several forms. Pollen grains may not grow on self-pollinated stigmas or may only grow slowly relative to foreign pollen, perhaps as a result of stigmatic secretions that harm the pollen. In some species, a chemical barrier on the stigma can only be broken down by foreign pollen. It has been shown in these cases that wounding the stigma mechanically, electrically, or chemically can remove the chemical barrier and allow self-pollination. Another common artificial way around this incompatibility is "bud pollination," in which the flower is carefully dissected before it opens and a self-pollination is performed. This method works because the chemical barriers are generally incompletely formed before the flower opens.

It is interesting to note that in situations where self-incompatibility is due to slow pollen-tube growth, self-fertilization is likely to occur when no other pollen is available. That is, it appears to be a "last-chance" way of producing seed. If any foreign pollen arrives on the stigma, it will win the race down the style and fertilize the ovule, but if no such pollen arrives, then the race goes to the slow self pollen. It has been suggested that this screening out of potential pollen by the stigma may also allow "competition" between different sources of foreign pollen. Perhaps plants that are genetically "good fathers" will have pollen tubes that grow faster.

Another way in which incompatibility may operate is through gametic incompatibility. In this case, the male and female gametes unite but do not form viable offspring. This mechanism is costly to the plant because it "loses" the ovule involved in gametic incompatibility. Similarly, endosperm incompatibilities (in which the embryo in the seed has no stored food) and production of sterile offspring, lead to wasted ovules. It seems unlikely that these mechanisms have evolved in response to selection for self-incompatibility. Instead, these are likely consequences of inbreeding and the increased probability of the expression of deleterious recessive genes.

To reiterate, mechanisms that prevent selfing are not mutually exclusive and two or more may occur together, as I have noted in several cases above. Such apparent redundancy is likely to represent relics from the pollination mechanisms of ancestral species, left in the course of further evolution. To understand properly the avoidance of self-pollination, one should take into account not only the fact that (in many species) the resulting seed is poor, but also that the wrong pollen may have immediate negative effects, in extreme cases resembling poisoning. In the evolution of pollination, economy plays a large role. Prevention of waste of pollen and especially eggs seems to be a legitimate consideration. The devices listed above therefore affect not only the pollination process proper but, even more prominently, the economy and prevention of nonsense or even deleterious pollination.

Table 3.1. Summary of possible adaptive values for various forms of sex expression.

Hermaphroditism, simultaneous
-- facilitates or eliminates mate finding
-- allows for sexual role versatility in unpredictable circumstances

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Hermaphroditism, sequential (protandry, protogyny)
-- enhances outcrossing
-- allows timing of different sexual functions for best functioning of male and female roles

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Monoecy
-- enhances outcrossing, but usually permits selfing also, and thus reduces problem of mate finding in harsh or isolated conditions
-- allows for sexual role versatility in unpredictable circumstances by allowing shifting floral sex ratios
-- permits placement of the two sexes of flowers for best functioning of male and female roles

Dioecy
-- enforces outcrossing
-- allows niche differentiation of different sexes
-- permits adjustment of progeny sex ratios