

Flower diversity and plant mating strategies

The diversification in form and function of flowers, the reproductive structures of angiosperms (flowering plants), provides some of the most compelling examples of adaptation by natural selection. Flowers vary enormously in size and display greater structural variation than the equivalent structures in any other group of organisms. This diversity provides outstanding opportunities for investigating the functional association between floral traits and plant mating. The recent integration of theoretical, comparative, and experimental approaches in evolutionary biology is giving rise to new insights into the relations between floral diversity and plant mating strategies.

Mating in plants. Mating is of profound evolutionary significance because it directly influences the amount and organization of genetic variation in populations and their responses to natural selection. Floral traits that influence mating are of particular importance because they govern not only their own transmission but also the transmission of all the other genes within the genome. Because most plants are hermaphroditic and produce multiple reproductive structures (flowers and inflorescences, segregated flower clusters), mating patterns can vary considerably among individuals, populations, and species. This variation can involve different rates of self- and cross-fertilization, levels of biparental inbreeding, and mate number resulting from multiple paternity. The complexity of plant mating can be revealed through the use of neutral co-dominant genetic markers, particularly allozymes (different forms of the same enzyme) and microsatellites (short repeated sequences of deoxyribonucleic acid). Such marker gene studies of mating patterns are a crucial prerequisite for determining the selective forces directing floral evolution and the diverse mating strategies that characterize flowering plants.

Floral diversity. Analysis of the relation between pollination and mating patterns is crucial for understanding the function and evolution of floral characters. This is because the selective forces determining reproductive diversification in angiosperms largely exert their influence through pollination and its effect on mating and fertility. Floral diversity in most angiosperm groups has been shaped by the evolution of adaptations associated with pollen vector type, the avoidance of inbreeding, and effective pollen dispersal.

Pollen vector divergence. Because plants are sessile, most floral diversity is associated with the particular vectors employed to achieve successful cross-fertilization. Pollen dispersal may occur via biotic (animals) or abiotic (wind and water) agents, resulting in contrasting suites of floral traits. Due to wide variations in morphology and physiology among animals, it is not surprising that adaptive radiations associated with pollen vector divergence are a prominent feature of many animal-pollinated families (for example, Orchidaceae, Polemoniaceae,

Scrophulariaceae). Recent work has focused on attempts to understand the ecological mechanisms responsible for evolutionary shifts from one pollinator group to another (for example, the evolution of bird pollination from bee pollination).

Flowers adapted for wind and water pollination exhibit less striking floral variation because of the absence of showy, attractive structures. However, even in abiotically pollinated groups, diverse structural mechanisms promoting successful cross-pollination are evident, although less is known about their biophysical characteristics and functional significance. Although wind pollination is known to have evolved from animal pollination in many angiosperm families, we are still largely ignorant of the microevolutionary forces causing this shift in pollination system.

Inbreeding avoidance. Not all floral diversity is directly linked to the particular agents of pollen dispersal. For example, considerable variation in the spatial and temporal arrangement of sexual organs is associated with mechanisms that reduce the harmful effects of self-fertilization (selfing) on plant fitness. Experimental studies of outcrossing species commonly demonstrate that offspring resulting from selfing exhibit reduced viability and fertility compared with those arising from cross-fertilization. The intensity of this fitness difference is particularly evident under field conditions, when plants are exposed to a full range of biotic and abiotic stresses. This phenomenon, known as inbreeding depression, largely results from the exposure of deleterious recessive alleles that are normally hidden from selection in the heterozygous condition in outcrossing populations.

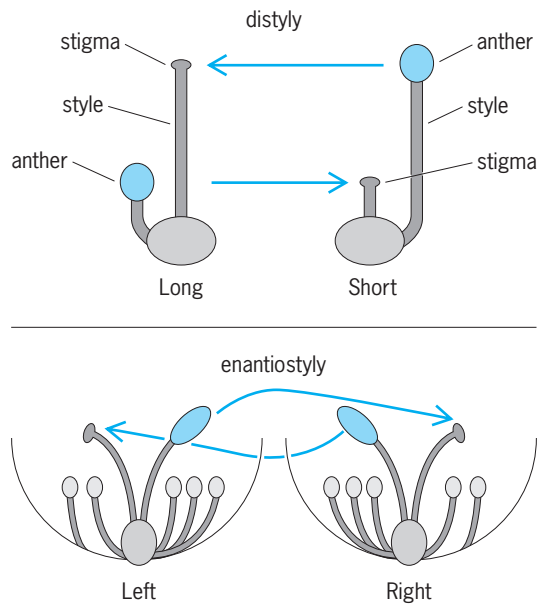


Fig. 1. Floral sexual polymorphisms distyly (a form of heterostyly) and enantiostyly. In distylous populations, two floral morphs occur: long (L)- and short (S)-styled. They differ reciprocally in stigma and anther height. Only cross-pollinations between the floral morphs result in seed set (arrows). In enantiostylous populations, two floral morphs occur, with styles deflected either to the left or right side (L and R morph, respectively) of the flower.

Inbreeding depression features in most theoretical models for the evolution of mating systems, and is widely recognized as a major selective force influencing reproductive traits.

Pollen dispersal. Because of the harmful genetic consequences of selfing, many plant species are protected from inbreeding depression through physiological self-incompatibility (in which pollen is unable to fertilize ovules of the same plant). Since self-incompatibility systems are essentially passive in nature, and therefore cannot influence pollen dispersal, most outcrossing species also possess floral mechanisms that actively promote pollen dispersal among plants. For example, in species with the sexual polymorphisms heterostyly and enantiostyly, the reciprocal placement of stigmas (pollen re-

ceivers) and anthers (pollen bearers) in the floral morphs promotes pollinator-mediated crosspollination between the morphs (Fig. 1). The positioning of sexual organs also reduces interference between female and male function in the same plant, resulting in less pollen wastage from self-pollination and more economical use of pollen. These sexual polymorphisms, therefore, reduce the sexual conflict that hermaphroditic plants encounter by achieving effective cross-pollen dispersal while avoiding sexual interference between female and male function.

In plants with large floral displays, such as mass-flowering trees and large clonal herbs, a considerable amount of selfing can potentially occur when pollinators transfer pollen grains among flowers on a single plant (geitonogamy). Geitonogamy removes pollen from the pool of male gametes available for cross-pollination, thus reducing fitness through male reproductive function (pollen discounting). It has recently been proposed that many features of floral design and display serve as “antidiscouping mechanisms,” reducing male gamete wastage and promoting fitness gain through outcrossed siring success. This hypothesis is challenging to investigate experimentally because of the difficulties in measuring pollen dispersal and male-outcrossed siring success in plants. Nevertheless, several recent experimental studies using genetic markers have provided convincing evidence that floral traits such as dichogamy (temporal segregation of female and male sex function) can function as antidiscouping mechanisms.

Evolutionary transitions. Spatial variation in ecological conditions and its influence on the local pollination environment elicit most evolutionary transitions in the reproductive biology of plants. Closely related species of angiosperms often possess different pollination and mating systems, indicating that plant reproductive traits can be evolutionarily labile (liable to change). Indeed, intraspecific variation in mating patterns is not uncommon, particularly in wide-ranging herbaceous species occupying diverse environments (for example, continents as well as islands). Two contrasting evolutionary changes to mating biology are particularly evident in flowering plants (Fig. 2). These transitions are the evolution of predominant self-fertilization (autogamy) from outcrossing and the evolution of dioecy (separate female and male plants) from cosexuality (hermaphroditism). Although these transitions involve strikingly different functional endpoints (for example, uniparental versus biparental reproduction), there is evidence that in animal-pollinated groups both can occur if populations encounter unsatisfactory pollinator service. This may at first seem paradoxical; however, it can be reconciled by recognizing that a plant’s pollination environment can be unsatisfactory in at least two distinct ways.

Changes in pollinator service. Insufficient pollinator service occurs when plants receive too few pollinator visits, resulting in pollen limitation of seed production and low fertility. If these conditions persist, genetic variants capable of autonomous

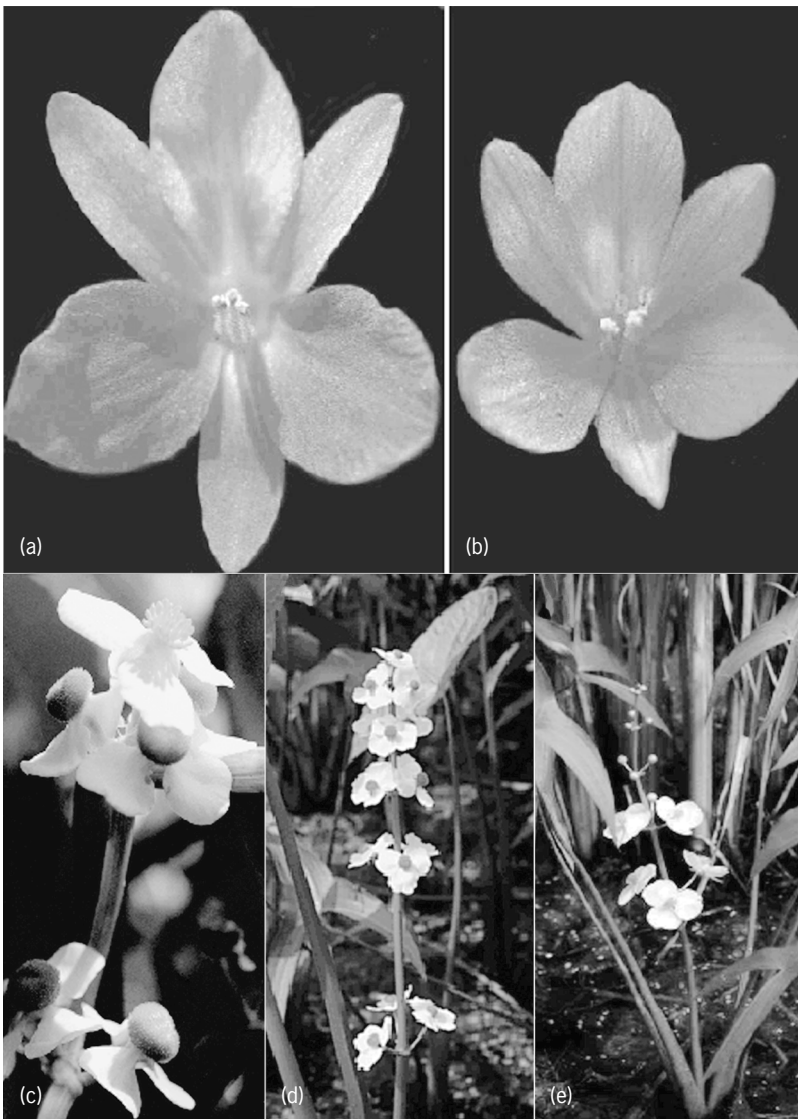


Fig. 2. Intraspecific variation in plant mating strategies. (a) Outcrossing and (b) selfing populations of the neotropical annual aquatic *Eichhornia paniculata* (Pontederiaceae) differing in flower size and showiness. (c) Hermaphroditic, (d) female, and (e) male plants of *Sagittaria latifolia* (Alismataceae), a North American clonal aquatic. Populations of this species are either monoecious [hermaphroditic plants with separate female (bottom of inflorescence) and male (top of inflorescence) flowers] or dioecious [separate female and male plants].

self-pollination will be favored, leading to the evolution of autogamy as a mating strategy. In contrast, inferior pollinator service results when sufficient pollination occurs to overcome pollen limitation, but the patterns of pollen dispersal result in offspring with low fitness because of increased selfing or biparental inbreeding. Models of the evolution of gender dimorphism indicate that if the product of the selfing rate (s) and inbreeding depression (δ) is >0.5 , unisexual mutants will spread, leading to the evolution of separate sexes (dioecy). Autogamy and dioecy are represented in many plant families, and each mating strategy is associated with a distinctive group of floral characters that arises by convergent evolution (that is, has multiple independent origins).

Evolution of selfing. The evolutionary pathway from predominant outcrossing to habitual selfing is the most well-known example of mating system evolution in plants. Selfing populations can be distinguished from their outcrossing progenitors by a suite of traits, including smaller flowers with reduced allocation to attractive structures, lower pollen production, and sex organs in close proximity, which promotes autonomous self-pollination. Selfers often occur in ecologically or geographically marginal sites with uncertain pollinator service, implicating reproductive assurance as the principal selection pressure causing this transition. Phylogenetic methods have enabled reconstruction of the evolutionary history of selfing, and in some genera this transition has originated on multiple occasions (for example, *Amsinckia*, *Eichhornia*, *Linanthus*). To understand whether selfing phenotypes will spread in outcrossing populations, it is necessary to have information on the pollination ecology of populations; the mode of selfing and its genetic basis; and the relations between selfing rates, inbreeding depression, and pollen discounting.

Evolution of dioecy. Although dioecy is the dominant sexual system in many animal groups, it is relatively rare in flowering plants. Approximately 7% of angiosperm species have separate female and male plants, yet this form of gender dimorphism is represented in nearly half of all angiosperm families. This distribution implies multiple independent origins of unisexuality. Comparative studies of trait correlations among angiosperm families indicate that dioecy is commonly associated with a suite of traits, including small, inconspicuous, white or green flow-

ers; pollination by wind, water, or generalist pollinators; fleshy fruits; and woody growth forms. Most dioecious species exhibit conspicuous sexual dimorphism, with male plants often producing larger flowers in greater numbers than female plants. Population sex ratios commonly deviate from unity, with male-biased sex ratios most often reported as a result of earlier flowering in males or greater mortality in females because of higher reproductive costs.

Models for the evolution of dioecy highlight the importance of a few key parameters, of which the most important are the selfing rates and inbreeding depression of ancestral cosexual populations, the genetics of sex determination, and the reallocation of resources to female and male function. Future empirical work on the ecological factors resulting in changes in pollinator service and the increased selfing required to drive the evolution of dioecy is required.

For background information see FERTILIZATION; FLOWER; PHYSIOLOGICAL ECOLOGY (PLANT); PLANT EVOLUTION; POLLEN; POLLINATION; REPRODUCTION (PLANT) in the McGraw-Hill Encyclopedia of Science & Technology. Spencer C. H. Barrett

Bibliography. S. C. H. Barrett, The evolution of mating strategies in flowering plants, *Trends Plant Sci.*, 3:335–341, 1998; S. C. H. Barrett, The evolution of plant sexual diversity, *Nat. Rev. Genet.*, 3:274–284, 2002; S. C. H. Barrett (ed.), *Evolution and Function of Heterostyly*, Springer, Berlin, 1992; S. C. H. Barrett and L. D. Harder, Ecology and evolution of plant mating, *Trends Ecol. Evol.*, 11:73–78, 1996; M. A. Geber, T. E. Dawson, and L. F. Delph (eds.), *Gender and Sexual Dimorphism in Flowering Plants*, Springer, Berlin, 1999; S. D. Johnson and K. E. Steiner, Generalization versus specialization in plant pollination systems, *Trends Ecol. Evol.*, 15:140–143, 2000; D. G. Lloyd and S. C. H. Barrett (eds.), *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants*, Chapman and Hall, New York, 1996; J. Lovett Doust and L. Lovett Doust (eds.), *Plant Reproductive Ecology: Patterns and Strategies*, Oxford University Press, 1988; M. T. Morgan and D. J. Schoen, The role of theory in an emerging new plant reproductive biology, *Trends Ecol. Evol.*, 12:231–234, 1997; R. Wyatt (ed.), *Ecology and Evolution of Plant Reproduction: New Approaches*, Chapman and Hall, New York, 1992.

Reprinted from the McGraw-Hill Yearbook of Science & Technology 2004. © Copyright 2004 by The McGraw-Hill Companies, Inc. All rights reserved.