The evolution of mating strategies in flowering plants

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Mating strategies in flowering plants are governed by several classes of floral adaptations. Floral design and display primarily influence the quantity and quality of pollen dispersed during pollination, whereas physiological mechanisms acting in the pistil screen pollen receipt by rejecting certain male gametophytes, especially self pollen. Selective mechanisms that influence the evolution of plant mating strategies include inbreeding depression, pollen discounting, and the optimal allocation of resources to female and male function. New insights on the origin, evolution and function of reproductive adaptations have come from integrating studies that link microevolutionary processes to macroevolutionary patterns.

The structural variation in flowers and inflorescences and different mechanisms for deployment of male and female gametes is remarkable when one considers that their sole function is to promote reproductive success. Analysis of any plant community reveals a variety of pollination and mating systems that coexist under apparently similar ecological conditions. Close relatives can reproduce in different ways just as unrelated taxa often share similar floral adaptations. How can biologists hope to make sense of this variation and the evolutionary processes responsible for the impressive reproductive versatility of flowering plants? A complete understanding of plant sexual diversity requires biologists to determine the physiological, developmental and molecular mechanisms that govern how reproduction occurs, and also to consider why particular reproductive adaptations have evolved.

Evolutionary biology provides the tools to solve this type of problem. Evolutionary studies of plant mating strategies employ three complementary approaches:

- Ecological and genetic experiments on populations focus on the selective mechanisms responsible for the evolution and maintenance of sexual traits, and the fitness consequences of particular mating patterns, especially the degree of inbreeding[1].
- Theoretical models identify key parameters that govern the dynamics of change in mating patterns and use optimality criteria to investigate evolutionarily stable reproductive strategies[2].
- Phylogenetic and comparative methods explore historical questions concerned with the evolutionary origins of reproductive systems and test adaptive hypotheses concerned with functional associations between traits and mating success[3].

Information from these approaches can be integrated in an effort to show how microevolutionary processes influence macroevolutionary patterns. Sexual traits are important in this regard because genes influencing reproduction govern their own transmission and that of all other genes in an organism. Shifts in mating pattern can therefore have profound influences on genetic variation, speciation and evolutionary diversification.

Research on the evolution of plant mating strategies has two main themes related to the evolution of combined versus separate sexes, and cross- versus self-fertilization. Both these dichotomies present their own particular challenges, but in each case the main objective is to determine the selective forces responsible for the evolution of one condition over another, or the maintenance of stable mixed strategies involving dual reproductive modes. An attractive feature of flowering plants is that many taxonomic groups display considerable inter- and intraspecific variation encompassing several reproductive systems. This variation allows for model building to predict conditions that favour shifts in reproductive mode and allows for direct testing of these models on the basis of the ecological and life-history associations that accompany these changes. The following review examines recent progress in studies on the evolution of mating strategies in flowering plants and provides a discussion of the concepts and terminology of the field (Box 1).

Distinctive features of mating in flowering plants

The character of mating in flowering plants is governed by distinctive features of the biology and ecology of the group. Immobility, modular growth, hermaphroditism and the closed carpel have all led to unique reproductive solutions. Because of their immobility, plants require vectors to transfer pollen, giving rise to diverse floral adaptations associated with the particular agents involved. Modular construction and the reiteration of flowers and inflorescences as reproductive units provides diverse opportunities for the deployment of male and female gametes in different spatial and temporal combinations. Variation in floral and inflorescence architecture involves hierarchical decisions on the optimal allocation of female and male reproductive effort[4]. Hermaphroditism provides opportunities for selfing, sometimes at the expense of outcrossing. Mechanisms that prevent selfing and its harmful effects[5] and promote more proficient pollen dispersal, have shaped much of floral evolution[6]. Finally, closed carpels, the defining feature of angiosperms, enables the selective screening of unsuitable male gametophytes. Competitive interactions among pollen tubes and the occurrence of diverse mechanisms of mate choice have evolved in association with the development of the style[7].

Another distinctive feature of flowering plants is their spectacular ecological radiation into virtually all habitats capable of sustaining plant growth. This has resulted in the evolution of diverse life histories ranging from short-lived ephemerals occupying transient habitats to woody species of more predictable environments that live for hundreds of years. What are the reproductive implications of this variation and, in particular, how are mating patterns influenced by life history? (Box 2). Recent comparative analysis of the relation between selfing rates and life form among angiosperm species indicates that as the duration of life cycles increase the probability of selfing decreases[3]. The traditional explanation of this pattern focused on the benefits to annual plants of selfing as a means of reproductive assurance. However, recent theoretical models on the costs of selfing in perennials provide an attractive alternative interpretation[8]. New insights into functional associations between mating strategies and life history have also been obtained from phylogenetic studies[3,9].

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Box 1. A glossary of terms in plant reproductive biology

Androdioecy: a sexual polymorphism in which populations are composed of cosexual and male plants. Very rare in flowering plants.

Cosexuality: condition in which plants reproduce as both maternal and paternal parents as a result of hermaphrodite sex expression. The commonest sexual system in flowering plants.

Dioecy: a sexual polymorphism in which populations are composed of female and male plants, usually differing in secondary sex characters. Often associated with large plant size and abiotic pollination.

Dichogamy: differences in the timing of anther dehiscence and stigma receptivity of flowers. Also occurs at the inflorescence or plant level and is common in flowering plants. Two types: protandry, with male function before female, and protogyny, with the reverse pattern. Generally reduces intraflower self-pollination.

Floral design: characteristics of individual flowers including their size, structure, sex condition, colour, scent, nectar production and degree of herkogamy and dichogamy.

Floral display: the number of open flowers on a plant and their arrangement within and among inflorescences. The important functional unit for pollination is usually daily inflorescence size.

Geitonogamy: mating that results from transfer of pollen between flowers on an individual. Common in mass-flowering species, genetically equivalent to selfing, and causes complete pollen discounting.

Gender strategies: concern the femaleness and maleness of individuals and reflect the relative contributions to fitness from maternal and paternal investment. Cosexual, female and male morphs are distinguished by their functional gender and co-occur in different sexual systems.

Gynodioecy: a sexual polymorphism in which populations are composed of cosexual and female individuals. Scattered distribution among angiosperm families but more common than androdioecy. Sometimes difficult to distinguish from subdioecy where populations composed of female, male and cosexual morphs.

Herkogamy: the spatial separation of anthers and stigmas within flowers. Common in flowering plants and, like dichogamy, generally reduces intraflower self-pollination.

Heterostyly: a sexual polymorphism in which populations are composed of two (distyly) or three (tristyly) cosexual morphs with reciprocal arrangements of anther and stigmas. Usually associated with heteromorphic incompatibility. The syndrome functions to promote more proficient pollen dispersal and to reduce selfing.

Inbreeding depression: the reduction in viability and fertility of inbred offspring in comparison with those from outcrossed matings. Results primarily from homozygosity of deleterious recessive alleles. Most strongly expressed in outcrossing species.

Mating system: the mode of transmission of genes from one generation to the next through sexual reproduction. Important determinants of plant mating systems are the maternal (ovule) selfing rate and male siring success through pollen (male fertility).

Monoecy: the condition in which plants produce separate female and male flowers. Prevents intraflower self-pollination and enables adjustment of female and male allocation to environmental conditions.

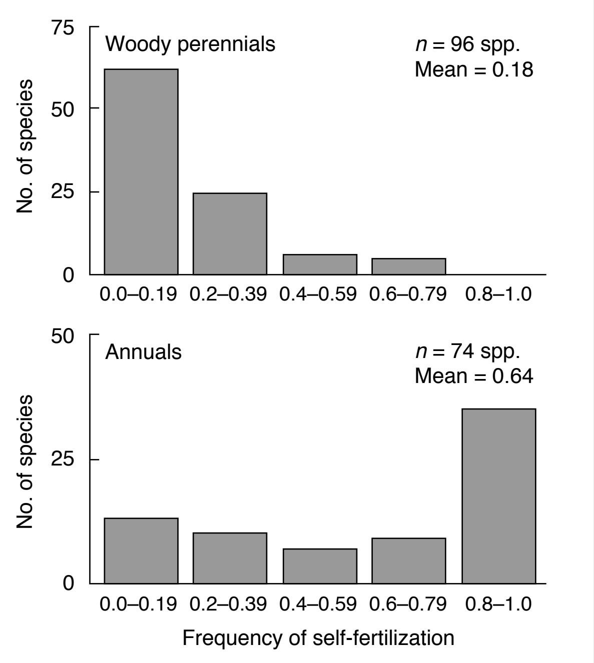
Pollen discounting: the loss in outcrossed siring success as a result of self-pollination. Reduces the transmission advantage of selfing and along with inbreeding depression represents the main costs of selfing.

Reproductive assurance: assured reproduction through selfing when conditions for outcrossing are unfavourable because of an absence of mates or pollinators. Requires plants to be self-compatible.

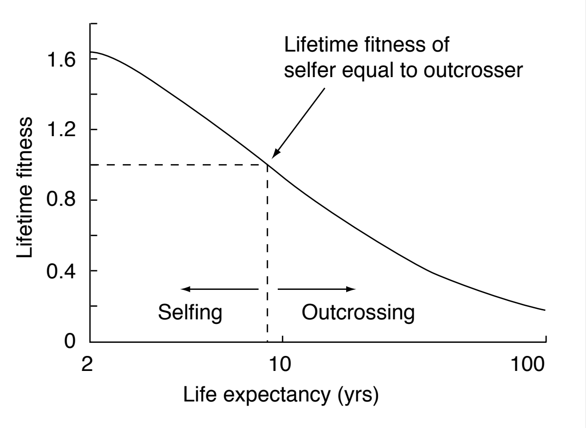
Self-incompatibility: the inability of a fertile cosexual plant to set abundant seed following self-pollination. Involves diverse physiological mechanisms that most commonly operate pre-zygotically. The most common anti-selfing mechanism in flowering plants.

Box 2. Mating systems and plant life histories

The segregation of genetic markers in naturally pollinated offspring from individual plants can be employed to estimate the incidence of self-fertilization in plant populations. Data on selfing rates can then be used to examine the relation between life history and mating system. Comparative data from diverse families (illustrated below) indicate that annual species self considerably more than woody perennials and, within families such as Polemoniaceae, repeated transitions from perenniality to annuality are accompanied by increased selfing[3].



Morgan and colleagues[8] have recently developed theoretical models that help explain these associations. They point out that previous hypotheses that focus on the importance of reproductive assurance in annuals do not help us understand why selfing rates in perennials are much lower than in annuals; common modes of selfing provide equal reproductive assurance to both annuals and perennials.



Instead, perennials may avoid selfing because of the cumulative effects of repeated bouts of adult inbreeding depression, and the costs to future survivorship and reproduction of producing additional selfed seed through reproductive assurance. Becaue of this, perennials pay a cost to reproductive assurance that annuals do not. *Figures modified, with permission, from Refs 3 and 8.*

As plants age, they grow larger with the number of flowers often increasing with each reproductive episode. What are the implications of mass blooming for plant reproduction, particularly in animal-pollinated species? Where pollinators favour large displays because of increased floral rewards, foraging within a single plant can result in considerable geitonogamous self-pollination. Geitonogamy is a largely non-adaptive consequence of adaptations for outcrossing and cannot be selected for directly[10]. A recent experimental study employing floral manipulations and allozyme markers in the mass-flowering clonal aquatic *Decodon verticillatus* (Lythraceae; Fig. 1a) revealed that approximately 82% of self matings arise from geitonogamy with only 18% resulting from within-flower selfing[11]. In this species, equivalent amounts of geitonogamy occur within flowering branches, between branches and between ramets through local foraging by pollinators (primarily bees).

Geitonogamy bears two potential mating costs. Most obviously, in self-compatible species, such as *D. verticillatus*, it can lead to selfing and inbreeding depression, thus reducing fitness as a maternal parent[12]. Another cost that has only recently been recognized is that pollen involved in self-pollination cannot be exported to other plants, reducing outcross male fertility and hence fitness as a paternal parent[13]. Since geitonogamy is probably ubiquitous in all but solitary flowered plants, this mating cost, termed 'pollen discounting'[14], seems likely to have been a powerful selective force on floral evolution influencing many aspects of floral design and display[6]. Many floral traits previously considered as acting to restrict selfing may function to promote fitness through enhanced pollen dispersal; this could explain the occurrence of these traits in species already protected from the harmful effects of inbreeding by self-incompatibility. Common features of floral design such as herkogamy and dichogamy, which reduce levels of self-pollination, can augment fitness through more proficient pollen dispersal to other plants.

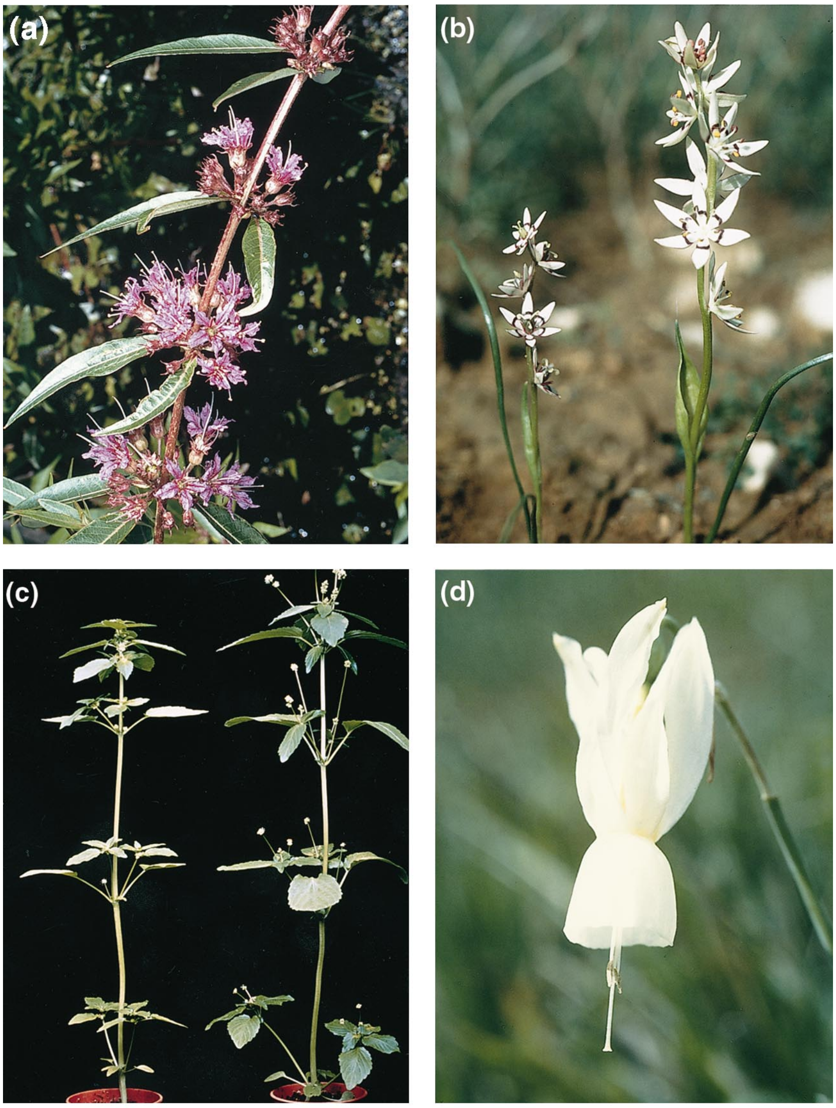


Fig. 1. Floral diversity and polymorphic mating strategies in flowering plants. (a) A long-styled morph of tristylous *Decodon verticillatus*. (b) Female (left) and male (right) morphs of dioecious *Wurmbea dioica*. Note the sexual dimorphism with larger, more showy flowers in the male compared with the female morph. Sexual selection involving male–male competition for pollinators is the most likely explanation for this difference. (c) Cosexual (left) and male (right) morphs of androdioecious *Mercurialis annua*. Note the elongated peduncles in the male morph, which function to promote more effective wind dispersal of pollen. (d) Flower of the long-styled morph of tristylous *Narcissus triandrus*, a species with late-acting ovarian self-incompatibility. *Photograph (a) courtesy of C.G. Eckert; photograph (c) courtesy of J.R. Pannell.*

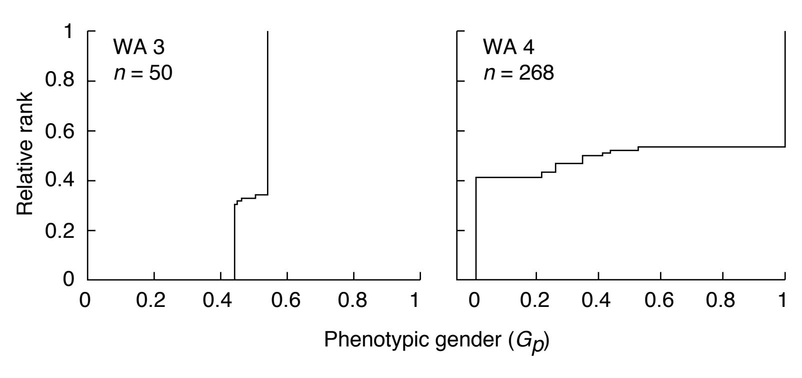
Gender strategies and the evolution of sexual systems

Male and female gametes are deployed in various structural and temporal combinations at the flower, inflorescence, plant or population level. The costs and benefits of various packaging options for gametes account for the complex array of gender strategies that occur. Most flowering plants have 'perfect' hermaphrodite flowers, although some are monoecious and others exhibit gender polymorphisms, the commonest of which are dioecism and gynodioecism.

Theoretical models attempt to explain the evolution of different sexual systems based on a few important parameters. These include inbreeding depression, the genetic control of the sex types and the optimal allocation of resources to female and male function[15]. An important challenge for theoretical work in this area, especially sex allocation models involving evolutionarily stable strategy approaches, is the inclusion of realistic features of plant life histories. For example, in classical allocation models, it is usually assumed that female and male reproductive allocation occur simultaneously from a fixed resource pool. This situation is unlikely for plants, where male allocation occurs at flowering and most female investment occurs later during seed maturation. Recent models involving temporal displacement of male and female allocation and trade-offs between growth and reproduction have provided novel findings that were not predicted by earlier theories[16]. Future models that include perennial life histories, modularity and hierarchical allocation are likely to provide further insights.

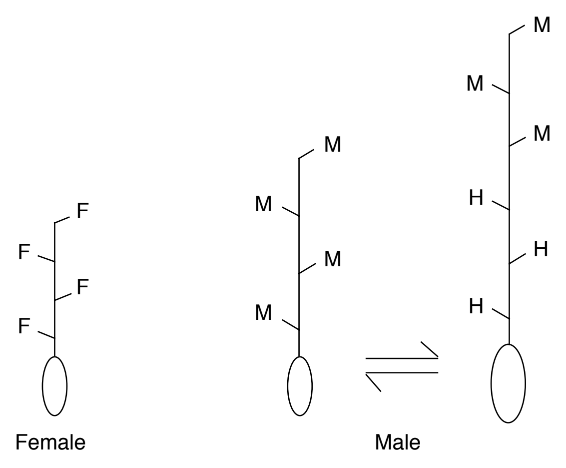
Box 3. Evolution of gender strategies in *Wurmbea*

Most dioecious plants show little intraspecific variation in gender. An exception is *Wurmbea*, composed of approximately 40 species native to Australia and Southern Africa. All African species are cosexual, whereas in Australia a range of gender strategies are evident, especially in *W. dioica*. In this diminutive fly-pollinated species, sexual systems range from cosexuality, through gynodioecy and subdioecy to full dioecy[26]. In Western Australia, cosexual and sexually dimorphic populations can be found growing together within a few metres of one another with reproductive isolation maintained by differences in flowering time. The phenotypic gender (G_p) of these populations are illustrated below.



The left plot is a sample of plants from a cosexual population, with most individuals bearing hermaphrodite, and rarely male flowers, and the right plot is a sample composed of male and female plants ($G_p = 0$ or 1, respectively), but with some male plants exhibiting sex inconstancy.

The propensity for male plants to produce hermaphrodite flowers is common in groups such as *Wurmbea*, in which sexual dimorphism evolves via the gynodioecious pathway[15]. Females often exhibit canalized gender, irrespective of environmental conditions, whereas male plants are labile in sex expression. Demographic studies[27] of *W. dioica* plants demonstrate that gender modification in males is size dependent, with larger plants able to bear the additional reproductive costs of maternal investment. The figure below illustrates the three sexual phenotypes that occur in subdioecious populations of *W. dioica*. Inflorescences arise from a corm and flowers are either female, male or hermaphrodite. The proximate genetic and physiological basis of these differences in sexual behaviour between the morphs is not known. Adaptive explanations concern the costs and benefits of producing pollen versus ovules in each morph. *Figures reproduced, with permission, from Refs 26 and 27.*



Gender in flowering plants can vary considerably among individuals as a result of both genetic and environmental factors, as in many cosexual species, or it can be highly canalized, as in dioecious species where most plants are either male or female regardless of growing conditions. Modularity and plasticity in reproductive allocations enable plants to modify their gender according to environmental conditions. An interesting observation is that as plants grow they often alter their gender in a predictable manner. Theoretical models predict size-dependent gender modification under various ecological circumstances[17]. Most models predict that relative allocation to female versus male function should increase with size, owing to the higher energetic costs associated with seed and fruit development, or differing size-dependent risks of mortality associated with female versus male reproduction[18]. Studies on animal-pollinated plants generally support this association (Box 3). However, the limited survey data for two families of wind-pollinated monoecious species (Asteraceae and Poaceae) suggest that relative allocation may become more male biased with increased size, perhaps because of greater fitness returns from more effective pollen dispersal by tall plants[19]. More comparative information from other wind-pollinated taxa is needed to determine whether an association between pollination mode and size-dependent allocation to female versus male function exists.

Comparative approaches are being used to investigate the association between morphological and ecological traits and the evolution of dioecy (for example among the Hawaiian flora[20]). An extensive survey[21], involving all flowering plant genera and families, found that dioecy occurred in about 6% of angiosperm species, and was most consistently associated with the presence of monoecy, wind or water pollination, and the climbing growth form. Insect pollination was under-represented among dioecious species and bird or bat pollination was negatively correlated with dioecy. Although most recent theoretical work has focused on the evolution of dioecy from cosexuality via the gynodioecious pathway[15], more attention should be paid to understanding the selective forces responsible for the shift to dioecy from monoecy and also the possibility of shifts in the opposite direction.

Although ‘global’ surveys can provide insights on trait correlations, they suffer from several problems. Because dioecy can evolve via several distinct evolutionary pathways[15], different trait associations will occur in some lineages and not others, so obscuring patterns when data are combined from many diverse families. In addition, intercorrelations make it almost impossible to determine which traits are functionally related to the evolution of dioecy without reconstructing the phylogenetic history of particular groups, and determining the specific order of establishment of individual traits. Few workers have used this approach to study the evolutionary origins of dioecy[22], although these methods have provided new insights on the evolutionary build-up and breakdown of another polymorphic sexual system – heterostyly[23,24]. Because of difficulties inherent in using comparative approaches[3,15], attention has focused on individual species that exhibit intraspecific variation in sexual systems. Although uncommon, such species provide attractive model systems for microevolutionary investigations of the selective mechanisms governing the evolution and maintenance of combined versus separate sexes.

Ecballium elaterium (Cucurbitaceae) is an herbaceous perennial with monoecious and dioecious populations in the Iberian peninsula[25]. Monoecious populations occur in northern wetter regions, and are replaced in the arid south by dioecious populations. The ecological basis of gender differentiation was examined in this species using reciprocal transplant experiments. Similar associations between aridity and sexual dimorphism are also evident in the Australian geophyte *Wurmbea dioica* (Colchicaceae)[26] (Fig. 1b; Box 3). These ecological correlations are also found in several other dioecious taxa, raising the possibility that stress conditions might promote the evolution of separate sexes in some groups. This might occur if cosexual plants are unable to maintain both sex functions under conditions in which resources are limited, or if inbreeding depression in cosexual plants is magnified under stress conditions, so favouring the spread of unisexuals.

A particularly striking example of intraspecific variation in sexual systems occurs in the ruderal weed *Mercurialis annua* (Euphorbiaceae)[28] (Fig. 1c). Dioecious, monoecious and androdioecious populations occur in different parts of Europe, and recent studies indicate that contrasting ecological and demographic conditions play a critical role in determining which sexual system is maintained. A novel feature of work on *Mercurialis* is the use of theoretical models of metapopulation dynamics to explain the advantages and disadvantages of combined versus separate sexes[29]. For species whose populations are short-lived and experience frequent colonization and extinction cycles, metapopulation models can provide new insights into the evolution of mating strategies[30]. This is because individual plants incapable of producing seeds by selfing cannot establish colonies on their own, and hence metapopulation processes select against unisexuality[29] and self-incompatibility[31].

Self-rejection mechanisms and the avoidance of inbreeding

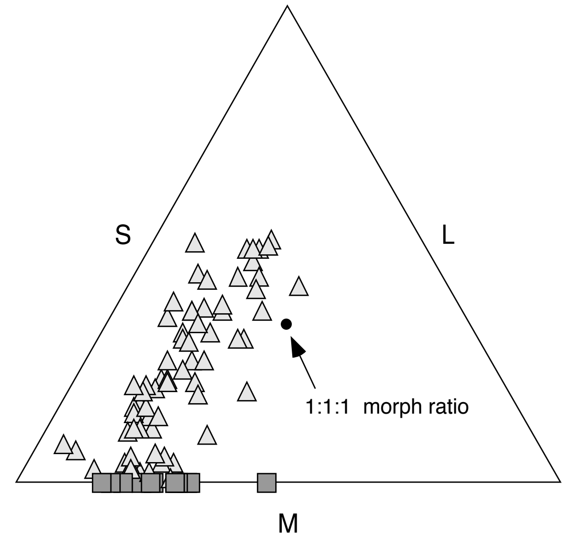
Morphological and phenological aspects of floral design and display primarily influence the quantity and quality of pollen dispersed during the pollination process. By contrast, mechanisms acting in the pistil screen unsatisfactory pollen by recognizing and rejecting specific male gametophytes, especially self-pollen or pollen from related individuals. The most common post-pollination mechanism serving this role is self-incompatibility (SI). Concepts of SI have broadened significantly in recent years, owing to the discovery of self-rejection mechanisms that do not fall readily into the traditional categories of SI[32,33]. Although it is well accepted that the primary function of all SI systems is to prevent inbreeding depression[5], the ways in which this is achieved involve a diversity of molecular and physiological mechanisms that operate at different stages in the mating cycle.

It is now clear that the most common SI systems (homomorphic SI of the gametophytic or sporophytic type), in which mating groups are morphologically identical, have evolved independently several times within flowering plants. Analysis of *S*-gene products in gametophytic Solanaceae and Papaveraceae and sporophytic Brassicaceae revealed that there are three different molecular mechanisms[34]. The stylar *S*-gene products in the Rosaceae, Scrophulariaceae and Solanceae have been cloned and found to be RNases. Phylogenetic analysis of *S*- and non-*S* RNases from angiosperms[35] indicates that the *S*-RNases from the Solanaceae and Scrophulariaceae are homologous but it is unclear whether *S*-RNases

Box 4. Evolution of sexual polymorphisms in *Narcissus*

Narcissus is composed of approximately 40 species of insect-pollinated perennial geophytes native to the Mediterranean. Little is known of their reproductive biology and genetics, despite their ornamental value. Species are either monomorphic, dimorphic or trimorphic for style length. Monomorphism and dimorphism are common in the genus whereas the trimorphic condition is restricted to *N. triandrus*[41].

Unlike species with conventional heteromorphic self-incompatibility, in *N. triandrus* intramorph crosses are fully compatible and hence plants can mate with all other plants in a population. In species with heteromorphic SI, morph frequencies at equilibrium are equal, whereas in *Narcissus* spp. markedly skewed ratios are a general feature of populations. Theoretical models involving asymmetric pollen transfer among the floral morphs can explain these curious ratios, which are summarized in the figure below, showing morph-ratio data from 80 populations of *N. triandrus* from Spain and Portugal[41]. Each population is represented by a single symbol (triangles, trimorphic; squares, dimorphic) positioned in the large triangle according to the morph frequencies in the population. The distance of a symbol to a given axis of the large triangle is proportional to the frequency of a morph in that population. A hypothetical population with equal morph frequencies is indicated. In contrast to other tristylous species in which populations with 1:1:1 morph ratios are common, in *N. triandrus* the L morph dominates in most populations and the M morph is absent from some.



Self-incompatibility (SI) in *N. triandrus* operates in the ovary and is not associated with differences in pollen-tube growth rates between cross- and self-pollen. Instead, SI results from a novel prezygotic phenomenon involving a reduction in the availability of fertile ovules, resulting from embryo sac degeneration following self but not cross pollination[32]. Differential responses of ovules after the two pollination treatments are evident well before pollen tubes enter ovaries suggesting 'long-distance' signalling events between pollen tubes and ovaries. These results imply that concepts of SI may need to be broadened to include a wider range of self-recognition mechanisms not only involving male gametophytic interactions in the stigma and style, but also aspects of female gametophyte development. *Figure redrawn, with permission, from Ref. 41.*

in the Rosaceae represent convergence or homology. PCR-based methods developed to survey *S*-allele sequence diversity in the Solanaceae provide a convenient technique to examine these problems in families with RNase-based SI (Ref. 36). It appears that sporophytic SI has multiple origins in flowering plants as every family known to exhibit this system is embedded in a clade with other familes with gametophytic SI and the families are often closely related (e.g. Solanaceae and Convolvulaceae)[37]. Sequence analysis has been used to estimate the origin of SI in Brassicaceae[38], and has revealed that the coalescence time for some *S*-alleles in *Brassica* is more than four times greater than the time since divergence of the species in which they occur. Many *S*-alleles maintained in natural populations of SI plants are probably of ancient origin as they share common features such as *trans*-specific evolution and high levels of sequence divergence.

Relatively little progress has been made in understanding the molecular basis of incompatibility for the other major class of SI systems (heteromorphic SI) involving the floral polymorphism heterostyly. In this system, plants are both self-incompatible and cross-incompatible with individuals of similar style type. This represents a more difficult problem, since the biochemical basis of self and cross rejection of pollen from like morphs is not known. A recent report of proteins specific to the pollen and styles of several distylous *Turnera* spp. (Turneraceae) is encouraging, because the bands revealed were only observed 24 h before flowering, indicating that they may be involved in the incompatibility reaction[39]. If this is true, it would be the first time that pollen and stylar incompatibility proteins have been identified in any species with heteromorphic SI. Even among homomorphic SI systems, where considerably more molecular analysis has occurred, there is still controversy over the identity of incompatibility proteins in pollen. Because heterostylous polymorphisms have evolved independently in at least 25 unrelated families, it is likely that several molecular mechanisms are involved and these may be quite distinct from those in homomorphic systems. Most work on heterostyly has focused on the study of natural populations using polymorphism as a tool to investigate adaptation, natural selection and genetic drift[40]. Future studies on the molecular genetics of heterostyly are needed to complement these evolutionary studies.

Recent investigations of wild species in the genus *Narcissus* (Amaryllidaceae) have revealed some unexpected findings that challenge commonly held views on both heterostyly and concepts of incompatibility in general[32,41] (Box 4; Fig. 1d). *Narcissus* exhibits a third class of self-incompatibility known as ovarian or late-acting SI in which self-rejection occurs after pollen tubes have entered the ovary, a much later stage than is normal for other SI systems[33]. Until recently this form of self-recognition was largely overlooked; however, recent work suggests that these systems are more common than previously thought, especially among woody families and taxa of monocotyledons. The major challenge for future studies of late-acting SI systems will be to determine their phylogenetic distribution, the genetic basis of mate recognition, whether rejection mechanisms occur pre- or post-zygotically, and to what extent the phenomenon is associated with the early abortion of developing embryos because of inbreeding depression.

The remaining group of post-pollination mechanisms that involve self-recognition represents a heterogeneous assortment including cryptic SI and other types of pollen–pistil interactions that involve the prepotency of cross versus self pollen. All tend to be facultative in operation, with the degree of outcrossing dependent on the size and composition of the pollen load on stigmas[42]. Many species considered to be self-compatible on the grounds of seed set from cross- versus self-pollinations, may possess these mechanisms as they can only be detected by using mixed pollinations involving genetically marked pollen. Virtually nothing is known about the genetics of these systems, nor whether they represent weaker versions of the classical forms of SI. This might provide mating flexibility under ecological conditions in which outcrossing cannot always be guaranteed.

Future prospects

The diverse mating strategies in flowering plants are a unique opportunity to investigate evolutionary patterns and processes at a variety of levels of biological organization. For many reproductive adaptations, there is a relatively straightforward link between genes, development, morphology and fitness, enabling integrative studies that bridge the molecular and ecological divide. Our understanding of reproductive biology is experiencing a major revolution, as the genetic consequences of different mating patterns are compared at the molecular level[43], and the genes controlling reproduction are being mapped[44], cloned and sequenced[45]. Such advances not only have important impacts on plant breeding and biotechnology, but will also strengthen the darwinian tradition of curiosity in plant mating strategies as a classic research paradigm for the study of evolution and adaptation.

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References

1 Barrett, S.C.H. and Harder, L.D. (1996) Ecology and evolution of plant mating, *Trends Ecol. Evol.* 11, 73–79

2 Morgan, M.T. and Schoen, D.J. (1997) The role of theory in an emerging new reproductive biology, *Trends Ecol. Evol.* 12, 231–234

3 Barrett, S.C.H., Harder, L.D. and Worley, A.C. (1996) The comparative biology of pollination and mating in flowering plants, *Philos. Trans. R. Soc. London Ser. B* 351, 1271–1280

4 Venable, D.L. (1996) Packaging and provisioning in plant reproduction, *Philos. Trans. R. Soc. London Ser. B* 351, 1319–1329

5 Jarne, P. and Charlesworth, D. (1993) The evolution of the selfing rate in functionally hermaphrodite plants and animals, *Annu. Rev. Ecol. Syst.* 24, 441–466

6 Harder, L.D. and Barrett, S.C.H. (1996) Pollen dispersal and mating patterns in animal-pollinated plants, in *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants* (Lloyd, D.G. and Barrett, S.C.H., eds), pp. 140–190, Chapman & Hall

7 Marshall, D.L. and Folsom, M.W. (1991) Mate choice in plants: an anatomical to population perspective, *Annu. Rev. Ecol. Syst.* 22, 37–63

8 Morgan, M.T. and Schoen, D.J. (1997) The evolution of self-fertilization in perennials, *Am. Nat.* 150, 618–638

9 Böhle, U-T., Hilger, H. and Martin, W.F. (1996) Island colonization and the evolution of the insular woody habit in *Echium* L. (Boraginaceae), *Proc. Natl. Acad. Sci. U. S. A.* 93, 11740–11745

10 Lloyd, D.G. (1992) Self- and cross-fertilization in plants. II. The selection of self-fertilization, *Int. J. Plant Sci.* 153, 370–380

11 Eckert, C.G. Contributions of autogamy and geitonogamy to self-fertilization in a mass-flowering, clonal plant, *Decodon verticillatus* (Lythraceae), *Ecology* (in press)

12 Eckert, C.G. and Barrett, S.C.H. (1994) Inbreeding depression in partially self-fertilizing *Decodon verticillatus* (Lythraceae): population genetic and experimental analyses, *Evolution* 48, 952–964

13 Harder, L.D. and Barrett, S.C.H. (1995) Mating cost of large floral displays in hermaphrodite plants, *Nature* 373, 512–515

14 Harder, L.D. and Wilson, W.G. A clarification of pollen discounting and its joint effect with inbreeding depression on mating-system evolution, *Am. Nat.* (in press)

15 Charlesworth, D. Theories on the evolution of dioecy, in *The Evolution of Gender and Sexual Dimorphism in Flowering Plants* (Geber, M.A., Dawson, T.E. and Delph, L.F., eds), Springer-Verlag (in press)

16 Seger, J. and Eckhart, V.M. (1996) Evolution of sexual systems and sex allocation in plants when growth and reproduction overlap, *Proc. R. Soc. London Ser. B* 263, 833–841

17 Klinkhammer, P.G.L., de Jong, T.J. and Metz, H. (1997) Sex and size in cosexual plants, *Trends Ecol. Evol.* 12, 260–265

18 Day, T. and Aarssen, L.W. (1997) A time commitment hypothesis for size-dependent gender allocation, *Evolution* 51, 988–993

19 Bickel, A.M. and Freeman, D.C. (1993) Effects of pollen vector and plant geometry on floral sex ratio in monoecious plants, *Am. Midl. Nat.* 130, 239–247

20 Sakai, A. *et al.* (1995) Biogeographical and ecological correlates of dioecy in the Hawaiian Flora, *Ecology* 76, 2530–2543

21 Renner, S.S. and Ricklefs, R.E. (1995) Dioecy and its correlates in the flowering plants, *Am. J. Bot.* 82, 596–606

22 Sakai, A.K. *et al.* (1997) Phylogenetic perspectives on the evolution of dioecy: adaptive radiation in the endemic Hawaiian genera *Schiedea* and *Alsinodendron*, in *Molecular Evolution and Adaptive Radiation* (Givnish, T.J. and Sytsma, K.J., eds), pp. 455–474, Cambridge University Press

23 Kohn, J.R. *et al.* (1996) Reconstruction of the evolution of reproductive characters in Pontederiaceae using phylogenetic evidence from chloroplast restriction-site variation, *Evolution* 50, 1454–1469

24 Schoen, D.J. *et al.* (1997) Evolutionary history of the mating system in *Amsinckia* (Boraginaceae), *Evolution* 51, 1090–1099

25 Costich, D.E. (1995) Gender specialization across a climatic gradient: experimental comparisons of monoecious and dioecious *Ecballium*, *Ecology* 76, 1036–1050

26 Barrett, S.C.H. (1992) Gender variation and the evolution of dioecy in *Wurmbea dioica* (Liliaceae), *J. Evol. Biol.* 5, 423–444

27 Barrett, S.C.H., Case, A.L. and Peters, G.B. Gender modification and resource allocation in subdioecious *Wurmbea dioica* (Colchicaceae), *J. Ecol.* (in press)

28 Pannell, J. (1997) Widespread functional androdioecy in *Mercurialis annua* L. (Euphorbiaceae), *Biol. J. Linn. Soc.* 61, 95–116

29 Pannell, J. (1997) The maintenance of gynodioecy and androdioecy in a metapopulation, *Evolution* 51, 10–20

30 Barrett, S.C.H. and Pannell, J. (1998) Metapopulation dynamics and mating-system evolution in plants, in *Molecular Systematics and Plant Evolution* (Hollingsworth, P., Bateman, R. and Gornall, R., eds), Taylor and Francis (in press)

31 Pannell, J. and Barrett, S.C.H. (1998) Baker's Law revisited: reproductive assurance in a metapopulation, *Evolution* 52, 657–668

32 Sage, T.L. *et al.* Differential ovule development following self- and cross-pollination: the basis of self-sterility in *Narcissus triandrus* (Amaryllidaceae), *Am. J. Bot.* (in press)

33 Sage, T.L., Bertin, R.I. and Williams, E.G. (1994) Ovarian and other late-acting self-incompatibility systems, in *Genetic Control of Self-Incompatibility and Reproductive Development in Flowering Plants* (Williams, E.G., Clarke, A.E. and Bruce Knox, R., eds), pp. 116–140, Kluwer

34 de Nettancourt, D. (1997) Incompatibility in angiosperms, *Sex. Plant Reprod.* 10, 185–199

35 Richman, A.D., Broothaerts, W. and Kohn, J.R. (1996) Self-incompatibility RNases from three plant families: homology or convergence? *Am. J. Bot.* 84, 912–917

36 Richman, A.D. and Kohn, J.R. (1996) Learning from rejection: the evolutionary biology of single-locus incompatibility, *Trends Ecol. Evol.* 11, 497–502

37 Holsinger, K.E. and Steinbachs, J.E. (1997) Mating systems and evolution in flowering plants, in *Evolution and Diversification of Land Plants* (Iwatsuki, K. and Raven, P., eds), pp. 223–248, Springer-Verlag

38 Uyenoyama, M.K. (1995) A generalized least squares estimate for the origin of sporophytic self-incompatibility, *Genetics* 139, 975–992

39 Athanasiou, A. and Shore, J.S. (1997) Morph-specific proteins in pollen and styles of distylous *Turnera* (Turneraceae), *Genetics* 146, 669–679

40 Barrett, S.C.H. (1992) Heterostylous genetic polymorphisms: Model systems for evolutionary analysis, in *Evolution and Function of Heterostyly* (Barrett, S.C.H., ed.), pp. 1–29, Springer-Verlag

41 Barrett, S.C.H. *et al.* (1997) Sexual polymorphisms in *Narcissus triandrus* (Amaryllidaceae): is this species tristylous? *Heredity* 78, 135–145

42 Cruzan, M.B. and Barrett, S.C.H. (1996) Post-pollination mechanisms influencing mating patterns and fecundity: an example from *Eichhornia paniculata*, *Am. Nat.* 147, 576–598

43 Liu, F., Zhang, L. and Charlesworth, D. (1998) Genetic diversity in *Leavenworthia* populations with different inbreeding levels, *Proc. R. Soc. London Ser. B* 265, 293–301

44 Bradshaw, H.D., Jr *et al.* (1998) Quantitative trait loci affecting differences in floral morphology between two species of monkeyflower (*Mimulus*), *Genetics* 149, 367–382

45 Münster, T. *et al.* (1997) Floral homeotic genes were recruited from homologous MADS-box genes preexisting in the common ancestor of ferns and seed plants, *Proc. Natl. Acad. Sci. U. S. A.* 94, 2415–2420

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