17 Ecology of Plant Reproduction: Mating Systems and Pollination

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> ...*That these and other insects, while pursuing their food in the flowers, at the same time fertilize them without intending and knowing it and thereby lay the foundation for their own and their offspring's future preservation, appears to me to be one of the most admirable arrangements of nature.*
>
> —Sprengel (1793)

INTRODUCTION

One of the main differences between most plants and animals is that the former cannot move in search of a partner to mate and thus needs a vector, which can be inanimate, such as wind or water, or an animal, vertebrate or invertebrate, to transport the male gametes (pollen) among flowers. This passivity has caused plants to evolve a great variety of adaptations,

either to disperse the pollen, for instance by attracting animal pollinators with a reward, or to become independent of pollen vectors, that is, by reproducing asexually or by self-pollinating.

This chapter focuses on the mechanisms by which plants are able to accomplish reproduction. We first describe how plants reproduce asexually and the advantages of sexual reproduction. Then we briefly review the different kinds of plant mating systems and what is known about their evolution, maintenance, and lability. The study of plant breeding systems addresses questions on the genetics of mating patterns, mainly associated with inbreeding depression and, until the last three decades, it was considered as a separate research line from that of pollination biology. The two areas have begun to merge into what has been called a new synthesis (Lloyd and Barrett 1996) or a new plant reproductive biology (Morgan and Schoen 1997) as floral biologists have enlarged their backgrounds with natural history, ecology, genetics, and theoretical approaches. The different systems of self-incompatibility, widespread among flowering plants, are treated briefly and the reader is referred to Nettancourt (1977), Barrett (1992), and Charlesworth et al. (2005) to explore this topic further. The paternal side of plant reproduction is increasingly receiving more attention in studies of reproductive success, and here we synthesize existing information on this subject, giving some directions for future research. For further readings about plant reproductive strategies and breeding systems we recommend Richards (1997) and de Jong and Klinkhammer (2005). Finally, we briefly review studies on the influence of pollinators on the evolution of floral traits and diversification of angiosperms.

ASEXUAL REPRODUCTION

Asexual reproduction is fairly common in plants and allows them to persist in their habitats with complete independence of pollinating vectors. Two types are distinguished, both quite similar from the genetic viewpoint, although their mechanisms are different: (a) vegetative reproduction, that is, asexual multiplication of an individual (genet)—which has originally arisen from a zygote—into physiologically independent units (ramets) (Harper 1977, Abrahamson 1980) and (b) agamospermy, the production of fertile seeds without sexual fusion of gametes. Advantages of asexual reproduction include the possibility to exploit larger areas and new locations, provided that vegetative propagules are widely dispersed (Janzen 1977, Lovett Doust 1981), and the preservation of successful genotypes since they are not lost during sexual recombination, which would be the case for example during heterozygote advantage (Peck and Waxman 1999). In many perennial plants, both asexual and sexual reproduction take place, the latter usually occurring once a growth threshold has been attained (e.g., Weiner 1988, Schmid and Weiner 1993, Worley and Harder 1996). A trade-off between asexual and sexual reproduction has been reported in a number of studies (e.g., Sohn and Policansky 1977, Law et al. 1983, Westley 1993) and can be influenced by plant size (Worley and Harder 1996), ramet density (Humprey and Pyke 1998), resource state of the growing site (Gardner and Mangel 1999), and population age (Sun et al. 2001).

VEGETATIVE REPRODUCTION

Vegetative reproduction is widespread among the angiosperms, especially in herbaceous perennials, but rare among the gymnosperms (possibly due to the predominantly woody habit of this group). Among woody plants, it is much more common in dwarf or creeping shrubs, climbers, and vines than in trees, although there are exceptions as, for example, the English elm (*Ulmus procera*) in Britain where all individuals are derived from one single cone (Gil et al. 2004). Vegetative reproduction is also quite conspicuous in anemophilous mono-cotyledons, and some species such as *Phragmites* and *Ammophila* occur in a specialized habitat throughout the world and are among the most widespread plant species known

(Heywood 1993). Vegetative reproduction is particularly successful in hydrophytes, probably because water is an adequate environment for the dispersal of relatively unprotected propagules, and invasive hydrophytes often cause severe environmental and economic problems. An example is *Caulerpa taxifolia*, a tropical green alga accidentally introduced into the western Mediterranean Sea in 1984, which has rapidly spread over a large area because of its efficient reproduction through stolons (Ceccherelli and Cinelli 1999).

The usual organs developed by plants to reproduce asexually are modifications of stems or axillary buds, which are stem initials. However, underground bulbs and corms are also common and have a protective function, especially during dormancy (hibernation or aestivation). Vegetative reproduction may be disadvantageous when a single clone occupies a large area, as the distance between individuals can be large and genetic variation is much reduced. The whole population may fail to set seed if the species is self-incompatible as in the case of bamboos or if it is diclinous as in the case of *Elodea canadensis* in Britain where all individuals are females. Clonal reproduction may also lose vigor with age, either due to an increased viral load through viral multiplication and reinfection or due to the accumulation of disadvantageous somatic mutations (Richards 1997). Furthermore, clonal reproduction is often more common in the margins of a species geographical range where environmental conditions limit seed set (Eckert 2002b).

AGAMOSPERMY

Agamospermy, asexual production of seeds, is a phenomenon absent in gymnosperms and limited to a small group (34 families) of angiosperms, occurring mainly in the Compositae, Gramineae, and Rosaceae (Asker and Jerling 1992, Richards 1997). It is highly polyphyletic, arisen on many occasions from sexual taxa, and examples of genera including both sexual and agamospermous species are *Taraxacum, Crepis, Hieracium, Sorbus*, and *Crataegus* (Nygren 1967). There are a few documented cases of evolution of agamospermy from different types of breeding systems such as autogamy (e.g., *Aphanes*), dioecy (e.g., *Antennaria, Lindera*), or heteromorphy (e.g., *Limonium, Erythroxylum*) (Berry et al. 1991, Richards 1997, Dupont 2002). Agamospermy can be sporophytic as in the case with *Citrus*, and the sporophyte embryo is then budded directly from the old sporophyte ovular tissue, usually the nucellus (adventitious embryony). However, more commonly is gametophytic agamospermy, where a female gametophyte is produced with the sporophytic chromosome number. Then the nonreduction of chromosome number results either from a complete avoidance of female meiosis (apospory and mitotic diplospory) or by a failure in it (meiotic diplospory) (Richards 2003).

It might seem as if production of seeds is assured in agamospermous species in the absence of pollination, but actually most species with adventitious embryony and apospory require the stimulus of pollination to fertilize the endosperm nucleus (pseudogamy). The seed habit, however, gives them the advantage of dispersal and the potential for extended dormancy, added to the possibility of fixing a successful genotype through asexual reproduction. Most agamosperms with apospory or adventitious embryony retain good pollen function, which can also be used in sexual reproduction. Within agamospermic species, both diploid individuals that reproduce sexually and polyploidy individuals that reproduce by agamospermy are usually found, but the capacity of both sexual and asexual seed production is very seldom found in the same individual (Bengtsson and Ceplitis 2000, Van Baarlen et al. 2000). The main disadvantage of agamospermy is that the cell line forms a gigantic linkage in which the advantageous genes cannot escape from the accumulated harmful ones. Moreover, such a cell line is unable to recombine novel advantageous mutants and thus cannot adapt to the new conditions after an environmental change, although some genetic variation can exist through somatic recombination (chromosome breakage and fusion), meiotic recombination, chromosome lose and gain, and accumulation of mutants (Richards 1997). That is probably

why truly obligate agamospermy, in which all possibility of sexuality has been lost, is rare (Asker 1980) and appears to be limited to a few diplosporous genera in which pollen is absent (unusual, as male-sterile mutants cannot be recombined). Even though a great deal of information has been accumulated on the origin, distribution, and mechanisms of agamospermy (e.g., Darlington 1939, Gustafsson 1946, Asker 1980, Berry et al. 1991, Richards 2003), much needs to be done yet to understand the evolution of this phenomenon and for the adequate interpretation of the observed patterns. Currently there is a great interest on the mechanisms underlying agamospermy because the possibility to select highly productive individuals and reproduce them asexually by seeds would imply an enormous potential for crop improvement (Ramulu et al. 1999, Bhat et al. 2005).

ADVANTAGES OF SEXUAL REPRODUCTION

The two most important characteristics of sexuality are (1) it creates genetic variability, through sexual fusion of gametes, chromosome segregation, and allele recombination and (2) it allows gene migration, so successful mutations can spread between generations and move within and between populations. Moreover, sexuality, and thus meiotic mechanisms, dissipates Müller's Ratchet (accumulation of harmful mutations), breaks up linkage disequilibrium, and also engenders zygotes that are free of virus (Richards 1997). Sexual reproduction is a primitive trait of nearly all eukaryotic organisms and has probably contributed to their success and long-term survival. The genetic variability gives sexual lines evolutionary potential to adapt to new conditions after an environmental change, a feature absent in asexual organisms as mentioned earlier. Sexuality is absent only in a few groups of animals that reproduce parthenogenetically, in agamospermous plants and in sterile (usually hybrid) plant clones. Here, we refer only to seed plants. The reproductive ecology of algae, bryophytes, and pteridophytes has been reviewed in Lovett Doust and Lovett Doust (1988).

The whole process of embryology in angiosperms (flowering plants) was already described in detail nearly half century ago by Maheshwari (1950). A good introductory chapter to the anatomy and physiology of sexual reproduction in both gymnosperms and angiosperms can be found in Richards (1997), and recent reviews on the origin and evolution of flowers are found in Doyle (1994) and Friis et al. (2005). The transition from a free-sporing heterosporous pteridophyte to a plant with gymnospermous reproduction, assessing adaptive explanations for the origin of seeds, is dealt with in Haig and Westoby (1989). According to these two authors, the first seeds would have originated from heterosporous species, the megaspores of which would have been selected for a larger size; the decisive character in their success would have been related to pollination, by evolving traits to capture microspores before dispersal of the megaspore. In pteridophytes, fertilization always takes place after gametes have been dispersed.

The gymnosperms, composed of five polyphyletic groups, are characterized by the ovule or seed borne externally (gymnosperm means naked seed), although they are greatly diverse in most reproductive structures. Two general features of their reproduction, relevant to the genetic structure of plant populations, are as follows:

1. There are no hermaphrodite cones. Thus, plants are either monoecious (separate sexes on the same individual plant; e.g., Pinaceae, Taxodiaceae) or dioecious (an individual plant has either all female cones or all male cones; e.g., Cycadaceae, Ginkgoaceae, Taxaceae), although some species have populations with both monoecious and dioecious members (Givnish 1980) and some previously reported monoecious Cupressaceae, such as *Juniperus phoenicea*, have shown to depart significantly from cosexuality (Jordano 1991 and references therein). If monoecious, there is usually dichogamy (separation in time of anther dehiscence from stigma receptivity), so outcrossing is always promoted.

FIGURE 17.1 The lizard *Podarcis lilfordi* pollinating the gymnosperm *Ephedra fragilis* on Dragonera Island (Balearic Archipelago). (Photo by Javier Rodriguez-Pérez. With permission.)

2. Pollination is almost always by wind (anemophily). Pollen grains in the Pinaceae even have two lateral air-filled sacs that act as wings, which allow them to fly very long distances. The genus *Ephedra* is an exception as it can be pollinated by insects (entomophily) and even by lizards in insular systems (Bino and Meeuse 1981, A. Traveset, personal observation of lizards and syrphid flies feeding on *Ephedra* flowers on Cabrera Island SE off Majorca) (Figure 17.1).

The reproductive ecology of gymnosperms has in general received less attention than that of angiosperms and we still need much more information on the former to infer about the genetic control of mating patterns within or between species. Ellstrand et al. (1990) reviewed the available data for genetic structure of gymnosperms, and concluded that they are generally highly diverse but have a low spatial differentiation. So far, there seems to be no evidence that nonangiosperms have low genetic diversity or that they are characterized by low gene flow (Midgley and Bond 1991, Brown et al. 2004).

Both gymnosperms and angiosperms have two major advantages over pteridophytes: (1) they do not depend on external water for sexual reproduction and (2) the zygote is protected within a seed, which in turn can be dispersed far from the parent plant. However, only about 750 species of gymnosperms exist today, in contrast to 10,000 pteridophytes. The major speciation has indeed occurred in the angiosperms, a group represented by over 220,000 species (Cronquist 1981). Such species richness is due to different factors (see Section "Diversification of Angiosperms"), of which perhaps the most important is the wider range of growth forms that allow them to inhabit a wider range of habitats than either pteridophytes or gymnosperms. The latter are mostly trees, which restrict the number of habitats where they can live, have limited breeding systems, limited pollination systems, and unspecialized seed dispersal (Givnish 1980). The development of a gynoecium (pistil) in the angiosperms (term meaning enclosed seeds) has probably been one of the most important steps in the evolution of plants.

Seed plants have a wide array of reproductive options that have evolved under particular environmental conditions (e.g., scarcity or absence of pollinators) and that are maintained or changed through the process of natural selection. Next, we focus on such reproductive options, on the factors that select for them and, briefly, on the genetic consequences for the plant population.

SELF-POLLINATION

Most angiosperms bear perfect flowers (containing both anthers and stigmas) and a large fraction of them are self-compatible and thus potentially selfing species (Bertin and Newman 1993, Vogler and Kalisz 2001). Estimates suggest that 62%–84% of temperate plants (mostly herbs) and 35%–78% of tropical plants (including shrubs, trees, vines, and herbs) are at least partially selfers (e.g., Arroyo and Uslar 1993). Comprehensive reviews of self-fertilization can be found in Jarne and Charlesworth (1993), Holsinger (1996), and Goodwillie et al. (2005) and several recent models have been developed to explain its evolution (e.g., Morgan et al. 2005, Porcher and Lande 2005, Scofield and Schultz 2006). Self-pollination can take place within a flower (autogamy) or between flowers of the same genet (geitonogamy). It is termed autonomous if the pollen is transferred to the stigma by various mechanisms not involving pollinators and facilitated if the pollen is transferred by a pollinator. The level of autogamy depends on the degree of separation between anthers and stigma (Table 17.1). Neither herkogamy nor dichogamy prevents geitonogamy, although they may reduce it considerably.

The level of geitonogamous crosses varies greatly both among and within species and depends mainly on pollinator foraging behavior and number of flowers of the same genet simultaneously open, since the time a pollinator spends in a patch usually increases with flower numbers (reviewed by Ohasi and Yahara 2001). It can also be affected by the architectural structure of the inflorescence (Jordan and Harder 2006). Geitonogamy reduces male and female fitness by reducing pollen export to other individuals, so-called pollen discounting, and by reducing the number of ovules available for outcrossing, so-called seed discounting. Geitonogamous pollination was for a long time called the neglected side of selfing (de Jong et al. 1993), but during the last decade it has received more attention by plant ecologists. Recent examples are studies of the effects of geitonogamy on evolution of dioecy (e.g., de Jong and Geritz 2002), sex allocation in hermaphrodites (de Jong et al. 1999), degree of selfing (Karron et al. 2004), and fruit set (Finer and Morgan 2003).

Plants have a variety of mechanisms to promote or prevent selfing. For example, the rapid wilting of pollinated flowers in some species has been suggested to be an adaptive regulation of the size of floral display to prevent geitonogamy (Harder and Johnson 2005). Herkogamy has evolved in plants that depend on animals for their pollination and dichogamy is found both in animal- and wind-pollinated species (for more details see Tammy et al. 2006). Dichogamy is found as often in species with self-incompatibility systems as in species without such systems (Bertin 1993). The reason for this could be that the different forms of dichogamy, protandry and protogyny, serve different functions. Protogyny is expected to be more efficient in preventing self-pollination and thus reducing inbreeding depression, whereas both protogyny and protandry are expected to decrease the interference between the male and the female functions (i.e., pollen and seed discounting). This theory was confirmed by Routely et al. (2004) who found protandry to be correlated to self-incompatible species and protogyny to be correlated to self-compatible species. Self-incompatibility is a mechanism preventing selfing that is known in about 30% of the angiosperm families; it is apparently controlled by a few loci, and it seems to have evolved independently several times (Jarne and Charlesworth

TABLE 17.1
Mechanisms of Plants to Avoid Overlapping of Male and Female Functions

Herkogamy: separation in space between anthers and stigma position
Dichogamy: separation in time between stamen dehiscence and stigma receptivity
    I. Protandry: the male phase is first
    II. Protogyny: the female phase is first

1993 and references therein). Male sterility (gynodioecy) and female sterility (androdioecy) are also mechanisms that reduce selfing and both might represent early steps in the evolution of dioecy (see Section "Sex Expression"). Cleistogamy is a mechanism that promotes selfing, as flowers do not open and can only self-fertilize. All species with cleistogamous flowers also produce hermaphrodite open-pollinated (chasmogamous) flowers (Lord 1981), and this appears to be evolutionarily stable under certain restrictive conditions (Schoen and Lloyd 1984, Masuda et al. 2001).

The immediate genetic consequences of selfing, and especially of obligate selfing, are a decrease in genetic variability commonly associated with high levels of homozygosity and, in the long term, the elimination of unfavorable recessive and partially recessive alleles, so-called purging (e.g., Barrett and Charlesworth 1991, Byers and Waller 1999, Crnokrak and Barrett 2002). In contrast to outcrossing organisms in which recombination generates variance among progeny, selfing species respond to changes in environments by interline selection (Jarne and Charlesworth 1993). The high levels of homozygosity usually cause a decrease in offspring quality, compared with the progeny of outcrossers. Such decrease is termed inbreeding depression, δ, and is considered as the major factor preventing self-fertilization. It was systematically studied by Darwin (1876), and much information has been gathered on its evolutionary consequences (e.g., Charlesworth and Charlesworth 1987, Holsinger 1991, Husband and Schemske 1996, Charlesworth and Charlesworth 1999). An increase in selfing is selectively favored if the progeny of selfing has a fitness greater than half that of the progeny produced by outcrossing.

There are three main factors that promote selfing and that are considered as explanations for the evolution of this breeding system:

1. *Reproductive assurance.* This is the factor that Darwin (1876) thought was the most important one for the evolution of selfing. Selfing has been classified as (1) prior, (2) competing, or (3) delayed, depending on the timing relative to a possible out-crossing event (Wyatt 1983, Lloyd and Schoen 1992). Delayed selfing takes place when the possibilities of cross-pollination have past and is therefore selected for despite the variation in outcross pollen availability, whereas the invasion ability of a prior selfing gene in a population depends on the variation in outcross pollination success (Morgan and Wilson 2005). Delayed selfing has been shown to increase seed set when pollinator visits are infrequent (Kalisz et al. 2004).

2. *Mating costs.* There are two kinds of outcrossing costs: (1) those referring to the transmission of genes and (2) those referring to the resources needed for copulation and pollination. Due to the higher parent–offspring relatedness in selfing compared with random mating, selfing alleles have a 50% transmission advantage (Jain 1976). This advantage, however, can be reduced by factors such as pollen discounting (Lloyd 1979). The energetic costs of producing large quantities of pollen, mainly in wind-pollinated plants, plus rewards such as nectar or oil for animal-pollinated ones, are relatively high in most species, and much greater in outcrossing than in highly autogamous plants, in which attractive structures (e.g., petals) and male reproductive functions are reduced (Jarne and Charlesworth 1993, but see Damgaard and Abbott 1995).

3. *Preservation of successful genotypes.* When environmental conditions are stable, selfing preserves the genotype adapted to those conditions. Evidence for the local adaptive hypothesis, which postulates that individuals perform better at their native site, whereas fitness of transplanted individuals declines with increasing distance, has been found for several plant species (e.g., Schmitt and Gamble 1990, Galloway and Fenster 2000, Joshi et al. 2001) though results are inconsistent with other plant species (references in Jarne and Charlesworth 1993, Jakobsson and Dinnetz 2005).

Data available so far on the breeding system of different species suggest that most outbreeders can also self-pollinate and most selfers can outcross as well, that is, that mixed mating systems are rather common in nature (Barrett and Eckert 1990). Furthermore, as might be expected, mixed mating systems appear to be more common in biotic than in abiotic pollinated species (Vogler and Kalilsz 2001). The range of outcrossing rates can vary greatly among populations of the same species, because of both genetic and environmental causes. For example, outcrossing rates in populations of *Aquilegia coerulea* vary with the abundance of pollinator groups (Brunet and Sweet 2006). Several models predict evolutionary stability of intermediate levels of selfing (reviewed in Goodwillie et al. 2005), although it is not clear yet how often evolutionary stability of mixed systems occurs in nature (Barrett and Eckert 1990, Plaistow et al. 2004). Intermediate selfing rates are expected to evolve in plants where selfing reduces either male or female fitness, for example, when there is pollen discounting (Cheptou 2004), or when competing selfing reduces the number of fertilized ovules (seed discounting) (Lloyd 1979). Mixed mating systems can also be maintained when there is an optimum pollen dispersal distance due to local adaptation (Campbell and Waser 1987) or when inbreeding depression affects dispersed progeny more than nondispersed progeny (Holsinger 1986). Further studies of correlations between flower traits, environmental variables, and mating systems are needed, and experimental approaches are crucial to discern if a character is a cause or an evolutionary consequence of the breeding system (e.g., Herlihy and Eckert 2004). In addition, further molecular studies (DNA sequence data, in particular) help to assess the consequences of selfing and outcrossing on genetic variability within and between populations.

SEXUAL EXPRESSION

There are a number of possibilities of how male and female organs can be distributed within a plant species, and this determines the levels of selfing and outcrossing (Table 17.2). For the last three decades, plant biologists have tried to understand the different evolutionary pathways that have led to the large variation in sexual systems found within flowering plants (reviewed by Barret 2002). Models of sex allocation (gain curves) have been used to investigate how male and female fitness change with increases in the allocation of limited resources to each sexual function (reviewed by Charlesworth and Morgan 1991). Sex allocation

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TABLE 17.2

Classification of the Different Possibilities by Which Male and Female Organs Are Distributed in a Plant Species

Hermaphroditism: all individuals (genets) have perfect flowers, all bearing functional stamens and pistils

Monoecy: the two sexes are found on all individuals, but in separate flowers

Andromonoecy: the same individual bears both perfect and male flowers

Gynomonoecy: the same individual bears both perfect and female flowers

Dioecy[a]: male and female flowers are on separate genets

Androdioecy[a]: male and hermaphrodite flowers are on separate genets

Gynodioecy[a]: female and hermaphrodite flowers are on separate genets

Subdioecy[a]: intermediate stage between monoecy and dioecy in which sex expression of males and females is not constant

Polygamy[a]: different combinations of males, females, and hermaphrodites are possible

[a] In these cases, when both male and female functions are not regularly found on the same genet, dicliny is said to occur.

theory alone, however, cannot explain all aspects of sex expression, such as, the spatio-temporal variation in sex expression found in nondiclinous plants (e.g., Solomon 1985, Emms 1993). The evolution of the various sexual systems found in plants may also be affected by gamete packaging (Lloyd and Yates 1982, Burd 1995) and selection for certain pollin-ation modes (Golonka et al. 2005). Furthermore, the combination of biogeographical data on diversity of sexual systems with phylogenies can help understand patterns of sexual diversification (Gross 2005).

MONOECY

Monoecy is widespread, especially in large wind-pollinated plants such as trees, sedges, and aquatic plants, and rarer in insect-pollinated plants (Richards 1997). At least in some floras this breeding system is associated with trees and shrubs that produce dry many-seeded fruits (Flores and Schemske 1984). One of the benefits of separate sexes on the same individual is that plants have the capacity to invest more on one sex or the other, depending on environ-mental conditions, to maximize the efficiency of both pollen dispersal and pollen capture. Moreover, monoecious plants benefit from a reduction of inbreeding depression, due to the spatial—and often temporal—segregation of sexes (Freeman et al. 1981). Evolutionary theories based on relative costs and benefits of male and female reproductive structures predict that plants growing under favorable conditions (larger in size, a greater resource supply, or a greater total reproductive effort) should invest relatively more in female than in male function (e.g., Freeman et al. 1981, Klinkhamer et al. 1997, Méndez and Traveset 2003). The opposite is often found for wind-pollinated plants, which have been found to increase relative maleness as patch quality improves (e.g., Burd and Allen 1988, Traveset 1992, Fox 1993). An explanation for this could be that large wind-pollinated plants may benefit from a relatively greater male investment if pollen is carried for longer distances (e.g., Smith 1981, Solomon 1989, Traveset 1992). However, Sakai and Sakai (2003) showed in a model that size and height in wind-pollinated cosexual plants may increase allocation to either male or female sex depending on several conditions, as for example plant density and number of small and large plants in the pollen dispersal area.

Models of sex allocation predict that the evolution of self-fertilization should result in a reduced allocation to (1) male function and (2) pollinator attraction (Charlesworth and Morgan 1991). In selfing monoecious plants, however, the investment to male function cannot be much reduced compared with hermaphroditic plants, as separate structures (petals, sepals, and pedicels) for male flowers and a higher production of pollen (to be transferred between flowers) are needed. Moreover, evolutionary changes in allocation patterns may be constrained by lack of genetic variation or by genetic correlations among characters (e.g., Ross 1990, Mazer 1992, Agren and Schemske 1995). More data on the importance of these genetic constraints, on the genetic and phenotypic correlations between allocations to both sex functions, and on the relationships between sex allocation, mating system, and repro-ductive success of the two sex functions are needed to understand the evolutionary dynamics of sex allocation. Long-term data on gender variation in natural populations are also necessary in studies of the evolution of sex expression (e.g., Primack and McCall 1986, Jordano 1991). There is much individual variation in patterns of sex allocation, and a variety of factors (reviewed by Goldman and Willson 1986) can cause a lack of consistent results. Variations at spatial and temporal scales in environmental conditions need to be considered, as gender expression of a species may vary, for instance, across a climatic gradient (Costich 1995). Documenting such variation at the individual, within-, and between-population level in the field is crucial to understand the selective pressures involved in the evolution of gender expression.

ANDROMONOECY

Andromonoecy is a breeding system that has been of particular interest in the study of sex expression patterns. It is uncommon, occurring in less than 2% of plant species (Yampolsky and Yampolsky 1922) and has probably evolved from hermaphrodite ancestors, by means of a mutation removing pistils from some perfect flowers and a subsequent regulation of male flower number (Spalik 1991) or by the production of staminate (male) flowers (Anderson and Symon 1989). According to resource allocation models, andromonoecy occurs in species in which the cost of maturing a fruit is great and the optimal number of male flowers is greater than the number of flowers that can set fruit (Bertin 1982, Anderson and Symon 1989, Spalik 1991). Pollen from male flowers can be more fertile than pollen from hermaphrodite flowers, as found in *Cneorum tricoccon* (Traveset 1995), representing an advantage to andromonoecy as this may increase both male and female fitness (Bertin 1982). By producing less-expensive staminate flowers, andromonoecious species may also increase floral display and hence attractiveness to pollinators (Anderson and Symon 1989). However, staminate flowers must not necessarily be less expensive, as in *Sagittaria guyanensis* ssp. *lappula* in which staminate flowers had more and larger anthers and also longer petals than hermaphrodite flowers (Huang 2003). Temporal differences in the functioning of male and female organs are a common feature of monoecious and andromonoecious taxa (e.g., Anderson and Symon 1989, Emms 1993). In the andromonoecious *Zigadenus paniculatus*, for instance, male flowers are produced at the end of the blooming period, when the returns on female allocation are small or nonexistent (Emms 1996). We need more data to test if these temporal patterns are adaptive and to answer questions such as: (1) how frequent are the mutations causing pistil loss? (2) is the production of surplus pistils advantageous (thus selecting against andromonoecy)? (see review in Ehrlén 1991), (3) does the rechanneling of resources from pistils to other structures (e.g., male flowers) increase fitness in hermaphroditic species? As claimed by Emms (1996), rather than asking why andromonoecy has evolved, it may be more interesting to ask why it is so rare. Moreover, to fully understand this breeding system, we also need to identify the factors that control male fitness. We need more data, for instance, on variation in pollen production per flower. We do not yet know if total pollen output in andromonoecious species is regulated through an increase in flower number or through the amount of pollen per flower. Data on a few species reveal that pollen grain number does not differ between male and hermaphroditic flowers (Solomon 1985, Traveset 1995, Cuevas and Polito 2004) or is even lower in males (Spalik 1991). Some authors have suggested that andromonoecy restricts outcrossing (Primack and Lloyd 1980, Bertin 1982, Narbona et al. 2002) whereas others argue that, depending on the pollinator, it may serve to reduce selfing (Anderson and Symon 1989).

Sex expression in andromonoecious species can be quite variable, among individuals, within and among populations, and through time (Diggle 1993 and references therein; Traveset 1995). Such variation can either be genetic or phenotypically plastic, varying with resource availability (e.g., light, water, nutrients available) (e.g., Solomon 1985, Diggle 1993). In andromonoecious species, staminate flowers are hermaphroditic in their early development and become mainly male by slower growth of the gynoecium compared with the androecium (Diggle 1992), and studies suggest that when resource levels are low the production of staminate flowers is favored (Calvino and Garcia 2005). Further supporting the connection between low resource status and staminate flowers is the finding that *Olea europea* produces staminate flowers in positions of the inflorescence that are less nurtured (Cuevas and Polito 2004).

GYNOMONOECY

Gynomonoecy is much rarer than andromonoecy, occurring only in about a dozen families, and there seems to be no satisfactory explanation yet for the difference in frequencies of these

two breeding systems. One possible reason may be the more expensive production of fruits compared with flowers (Charlesworth and Morgan 1991). Recent studies suggest that the benefits of this breeding system lies in the promotion of outcrossing and increase in pollinator attractiveness, rather than in the flexibility in allocation of resources to either female or male function (Bertin and Gwisc 2002, Davis and Delph 2005).

DIOECY

Dioecy is found in a large proportion of gymnosperms (c.52%; Givnish 1980) compared with angiosperms (c.6%; Renner and Ricklefs 1995), and appears to be strongly associated with woodiness in certain tropical floras (e.g., Givnish 1980, Sakai et al. 1995). The incidence of dioecy varies notably among regional floras, ranging from values as low as 2.6% (Balearic Islands) or 2.8% (in California; Fox 1985) to c.15% in the Hawaiian flora (Sakai et al. 1995). This mating system has evolved independently many times, as suggested by its scattered systematic distribution (Lloyd 1982). Dioecy has been found to be associated with monoecy, wind and water pollination, and climbing growth (Renner and Ricklefs 1995) as well as with tropical distribution, woody growth form, plain flowers, and fleshy fruits (Vamosi and Vamosi 2004). The two major evolutionary pathways for the origin of dioecy are via monoecy (Yampolsky and Yampolsky 1922, Dorken and Barrett 2004) and gyno-dioecy (Freeman et al. 1997, Weiblen et al. 2000), although it has also evolved from androdioecy, as in the genus *Acer* (Gleiser and Verdú 2005) and from distyly in several angiosperm genera (Beach and Bawa 1980). The monoecy pathway has been described as a gradual divergence in the relative proportions of male and female flowers in the two incipient sexes (Charlesworth and Charlesworth 1978, Ross 1978, 1982, Lloyd 1982) and is presumably easier than the evolution of dioecy via other mating systems, as mutations affecting pollen or ovule production have already occurred in the unisexual flowers (Renner and Ricklefs 1995).

The classic hypothesis on the mechanism underlying the evolution of dioecy states that it has evolved to overcome the negative effects of inbreeding depression (Thomson and Barrett 1981, Charlesworth 2001, de Jong and Klinkhammer 2005). The frequently documented association between dioecy and abiotic pollination with its imprecise pollen movement supports this view (references in Renner and Ricklefs 1995). Another school of thought believes that dioecy is the outcome of sexual selection (Willson 1979, Armstrong and Irvine 1989), suggesting that separation of sexes may result in a more efficient use of resources for both male and female functions. Freeman et al. (1997) argue that both schools are correct but that the mechanisms act on taxa with different life histories and different historical contexts. These authors hypothesize that in self-incompatible species dioecy has resulted from selection for sexual specialization, whereas in self-compatible species dioecy would have evolved via gynodioecy, a route that involves a genetic control of gender. According to them, the pathway toward dioecy via monoecy (especially common in wind-pollinated species) might be more controlled by ecological factors, since sex-changing and sexual lability occur mostly among species that arose by this pathway and not via gynodioecy.

The possibility that differential predation (specifically, seed predation or flower herbi-vory) could be another force selecting for dioecy was hypothesized a long time ago (Janzen 1971), and sex-related differences in herbivore damage have been reported for some species (see reviews in Watson 1995, Ashman 2002, Cornelissen and Stiling 2005). Seed dispersal has also been suggested to influence evolution of dioecy (Thomson and Brunet 1990), and a recent model showed that dioecy has negative effects on seed dispersal, resulting in a more clumped distribution of seeds since they are only produced by females (Heilbuth et al. 2001). In addition, pollen dispersal can be negatively affected in those dioecious species that have been found to have segregated spatial distribution for the different sexes (Eppley 2005).

Some plants are cryptically dioecious, that is, they are morphologically hermaphrodite but functionally dioecious, since either males or females, or both, have sterile or disfunctional opposite-sex structures (reviewed by Mayer and Charlesworth 1991, Verdú et al. 2004). Other species are classified as subdioecious, with populations possessing strictly male or female functions and a variable proportion of hermaphrodites; such proportion may vary depending on how favorable growing conditions are, as found in *Schiedea globosa* (Sakai and Weller 1991).

GYNODIOECY

The overall frequency of gynodioecy is generally considered to be low (Yampolsky and Yampolsky 1922, Lloyd 1975), although recent studies have shown that it has been overlooked. For females to be maintained in the population, their lack of male function has to be compensated with a higher female fitness (a higher quantity and quality of seed production). Sex allocation models predict that female fitness has to be at least twofold of that of hermaphrodites, if inheritance of male sterility is governed by nuclear genes, though it can be less than double when both nuclear and cytoplasmic genes control gender (Lloyd 1975). This compensation has been found in several gynodioecious species such as *Cucurbita foetidissima* (Kohn 1988), *Geranium maculatum* (Agren and Willson 1991), *Chionographis japonica* (Maki 1993), *Prunus mahaleb* (Jordano 1993), and *Opuntia quimilo* (Diaz and Cocucci 2003), but was not found in *Kallstroemnia grandifolia* (García et al. 2005). Cytoplasmic genes that produce females by causing male sterility is the most common cause of gynodioecy, and the balance between such genes and nuclear restorer genes that restore pollen production is crucial for the maintenance of gynodioecy in populations (reviewed by Jacobs and Wade 2003 and modeled by Bailey et al. 2003). The evolution of this breeding system has usually been interpreted as an escape from inbreeding depression, and this may actually be the main selective factor in species such as *C. japonica* (Maki 1993). However, factors other than inbreeding avoidance select for gynodioecy in other species (e.g., *Ocotea tenera*; Gibson and Wheelwright 1996). Variation in resource allocation to floral organs as corolla size (Eckhart 1992), anther size, and nectar production (Delph and Lively 1992) between females and hermaphrodites might also be important in the evolution of gynodioecy.

ANDRODIOECY

One of the first observations of functional androdioecy was made in *Datisca glomerata* (Liston et al. 1990) and it is still being documented in fewer occasions than gynodioecy (Pannell 2002). Androdioecy is most likely to evolve from dioecy (Pannell 2002), and pollen limitation has been suggested as the mechanism underlying the transfer between these breeding systems (Wolf and Takebayashi 2004). In a recent model, Pannell and Verdú (2006) point out that androdioecy also could evolve from heterodichogamic hermaphrodite populations. It is probably the requirements for its maintenance, predicted by sex allocation theory, which makes it a rare and evolutionarily unstable breeding system. Models predict that the frequency of male plants should be much lower than that of hermaphrodite plants and the siring success of the former should be at least twice as high (Lloyd 1975, Charlesworth 1984). *Phillyrea angustifolia* is reported to have both functional androdioecious and functional dioecious populations in southern France, and contrary to predictions no difference in number of seeds sired has been found between hermaphrodite males and pure males (Traveset 1994, Vassiliadis et al. 2002). In *Mercurialis annua*, androdioecy was found to be stable within a metapopulation context, females within populations were always selected for, but during founding of new populations the hermaphrodite individuals had advantages over females as these were not able to breed properly (Pannell 2001).

Many of the previously cited androdioecious species have shown to be dioecious after closer inspection of the functionality of the breeding system. Thus, it is necessary to go deeper into the functionality of this breeding system and to document that hermaphrodites produce viable pollen that sire a significant number of progeny.

SELF-INCOMPATIBILITY SYSTEMS

Systems of self-incompatibility are widely distributed among flowering taxa and have been recorded from approximately 20 orders and over 70 families of dicots and monocots, with different life-forms, and from tropical as well as temperate zones (Barrett 1988). Here we briefly review the major classes of self-incompatibility, their general properties, and the hypotheses to explain the evolution of some of these systems.

Self-incompatibility systems can be heteromorphic where morphological differences can be seen on the sporophyte as two (distyly) or three (tristyly) mating types that differ in style length, anther height, pollen size, and pollen production. They can also be monomorphic where the preventing of selfing relies on a chemical–physiological response. Monomorphic systems (see reviews in Franklin-Tong and Franklin 2003, Hiscock and McInnis 2003) can be (1) gametophytic and expressed during pollen tube growth coded by the haploid genotype of the pollen tube, as found for instance in Solanaceae and Papaveraceae or (2) sporophytic and governed by the genotype of the pollen-producing plant and transferred as proteins to the pollen grain coat, as found in the Brassicaceae (Castric and Vekemans 2004 and references therein). Monomorphic and heteromorphic systems do not seem to co-occur in the same plant families, except for the Rubiaceae (Wyatt 1983).

In monomorphic systems, pollen and pistil incompatibility is controlled by different but tightly linked genes, the S-locus (self-incompatibility locus) that should rather be called the S-genes complex (Schopfer et al. 1999, Takasaki et al. 2000, Castric and Vekemans 2004). Pollen tube growth is inhibited in the style (in most gametophytic systems) or in the stigmatic surface (in most sporophytic systems). Inhibition in the ovary, so-called late-acting incompatibility is also common, although when the rejection is postzygotic it is difficult to discern its effect from inbreeding effects (Seavey and Bawa 1986). It is also difficult to separate between inbreeding effects and self-incompatibility in species where self-incompatibility is cryptic, that is, where tube growth rate is greater for cross- than for self-pollen, such as *Cheiranthus cheiri* (Bateman 1956 in Barrett 1988), and *Dianthus chinensis* (Aizen et al. 1990). Gametophytic incompatibility systems have evolved independently several times in the angiosperms (Steinbachs and Holsinger 2002, Charlesworth et al. 2005) and work with very different mechanisms (Franklin-Tong and Franklin 2003).

Heterostyly is governed by a single locus with two alleles, in distylous species, or by two loci each with two alleles and epistasis operating between them in tristylous plants. Heterostyly also has a polyphyletic origin and has been reported from about 25 families of flowering plants (Barrett 1990). The most visible trait in heterostylous plants is the significant difference between morphs in the height at which stigma and anthers are positioned within the flowers. This polymorphism is usually associated with a sporophytically controlled diallelic self-incompatibility system that prevents self- and intra-morph fertilizations, but not all heteromorphic species are self-incompatible (e.g., Casper 1985, Barrett et al. 1996). Herbaceous heterostylous taxa such as *Primula*, *Oxalis*, *Linum*, and *Lythrum* have received much attention in molecular studies since long ago (references in Barrett 1990), although mostly in controlled experimental conditions. In the last decades, a number of studies on population biology, and on structural, developmental, and physiological aspects of heterostylous species have been carried out, and much information has been accumulated on the function and evolution of heterostyly (comprehensively reviewed in Barrett 1992 and in de Jong and Klinkhammer 2005). Different hypotheses have been formulated on the sequence of

evolutionary events in heterostylous plants. The classic model (Charlesworth and Charlesworth 1979) assumes that inbreeding avoidance has selected for a diallelic self-incompatibility, followed by evolution of reciprocal herkogamy and appearance of the different floral polymorphisms to increase the efficiency of pollen transfer between incompatible morphs. This was challenged by Lloyd and Webb (1992), who believe that reciprocal herkogamy evolved first as a result of selection to increase the efficiency of pollen transfer, and that self-incompatibility appears later as a gradual adjustment of pollen tube growth in the different morphs. The hypothesis of Lloyd and Webb, in fact, supports Darwin's idea that the style-stamen polymorphism acts as promoter of disassortative pollination, and evidence for it is accumulated in studies of pollen deposition patterns on the stigmas of the different morphs (Kohn and Barrett 1992, Lloyd and Webb 1992). Some authors (e.g., Olmstead 1986), however, see self-incompatibility independent of the level of inbreeding in the population as a whole, and argue that inbreeding is more influenced by small effective population sizes than by selfing avoidance.

PATERNAL SUCCESS

For many years, studies of plant reproductive success were strongly biased by examining only the female function (see review in Willson 1994, Schlichting and Delesalle 1997). However, in the last three decades, different aspects of male reproductive success, such as pollen production, pollen removal, and paternity of offspring, have been examined in a number of studies (see reviews in Snow and Lewis 1993, Ashman and Morgan 2004). Male fitness is usually expressed in terms of the number of sired offspring surviving to reproductive age. As this is very difficult to measure, and has to be indirectly estimated from genetic markers, correlates of fitness such as pollen germination ability, pollen tube growth rate, ability of pollen to affect fertilization, weight and number of seeds sired, seed germination, and performance of sired seedlings are usually evaluated. This far, most pollen competition studies with heritable markers have been hand-pollination studies with known pollen donors, and allozymes have been used for diagnosing parental identity (reviewed in Bernasconi 2003). The development of more variable molecular markers in combination with statistical models to assess male reproductive success will hopefully help to understand fitness returns from investment in male function (e.g., Barrett and Harder 1996, Smouse et al. 1999, Burczyk et al. 2002).

Resources allocated to male function are in turn divided among number and size of pollen grains, male accessory structures (e.g., petals, sepals, bracts), and substances (e.g., nectar). Such resource allocation may be linked to male fitness, although we still have little experimental evidence supporting this (see examples in Bertin 1988, Young and Stanton 1990). When measuring male fitness, it is important to quantify pollen removal and also to monitor the success of removed pollen as these two variables may not be positively correlated (e.g., Wilson and Thomson 1991, but see Conner et al. 1995). For instance, a bee removing much pollen from a nectar-rich plant may fly short distances or promote much geitonogamy, which may limit potential gains in male fitness. The success of the removed pollen is influenced by the percentage of pollen grains germinating, by the rapidity of germination on the stigma, and by pollen tube growth rate in the style, all of which in turn are affected by abiotic factors, especially temperature (Bertin 1988, Murcia 1990). The success of a particular pollen grain also depends on the composition and size of the whole pollen load on the stigma. Several studies on pollen tube growth rate have found that the presence of self- or incompatible pollen has a negative effect on tube growth of cross-compatible pollen (e.g., Shore and Barrett 1984). The competitive ability of a pollen grain is influenced by its own genotype, which differs among individuals and among pollen grains

from the same individual. Thus, the genotype of all pollen grains on the stigma influences the success of a particular one (e.g., Bookman 1984). Large pollen loads can be advantageous over small loads because the former are more likely to enhance pollen germination as well as tube growth rate (e.g., Ter-Avanesian 1978). However, large pollen loads may yield fewer pollen tubes per pollen grain than small loads (Snow 1986) and, thus, the probability that a certain pollen grain is represented in the seed crop can also be lower for large pollen loads. The sequence of pollen deposition on the stigma has also shown to be important determining the proportion of seeds sired by the different pollen grains (e.g., Mulcahy et al. 1983) and it affects the potential for interaction (competition) among grains, which may have been brought by different pollinators (e.g., Murcia 1990). In a study on *Hibiscus moscheutos*, Snow and Spira (1996) gave strong evidence that pollen tube competitive ability varies among coexisting plants, arguing that it may be a relevant component of male fitness in plants. Pollen grains from different donors on the stigma not only race for access to ovules (exploitation competition) but can also interfere with the germination and growth of each other (interference competition), as it has been found in wild radish (Marshall et al. 1996) and in *Palicourea* (Murcia and Feinsinger 1996).

For hermaphroditic plants, the male function has been predicted to be limited by mating opportunities and not by resources, whereas the opposite is expected for the female function. This hypothesis has been termed the fleurs-du-mâle hypothesis (Queller 1983), also known as the male function or pollen donation hypothesis (PDH) (e.g., Fishbein and Venable 1996, Broyles and Wyatt 1997). According to the PDH, large floral displays would especially benefit the male function as they would have a greater fraction of their pollen exported. Some authors even believe that flower number in the angiosperms has been selected by such male function (e.g., Sutherland and Delph 1984). Several variants of the PHD have been formulated and are reviewed by Burd and Callahan (2000). These authors propose that the PHD should explain the evolution of excessive (nonfruiting) flowers, not total flower number, and that studies should consider the whole plant fitness, not only the fitness of single flowers or inflorescences. It is also possible that excessive flowers have a positive effect on the female function, by enhancing the reception of larger amounts of outcross pollen (Burd 2004). More studies with adequate experimental designs and controlling for variables such as level of resources are needed to determine whether male function does select for large floral displays. We must also know the consequences of self- versus cross-pollination, as large floral displays may be less efficient at exporting pollen if pollinators promote geitonogamy (de Jong et al. 1993). Theoretically, if female fitness (achieved via fruit production) is less affected by geitonogamy than male fitness (achieved via siring of fruits on other plants), we would predict that small plants invest more in male reproduction whereas large plants emphasize more on the female function. Some data seem to support this prediction (de Jong et al. 1993, 1999).

By evaluating both female and male reproductive success, it is possible to examine (1) whether they are correlated or not, (2) the genetic variation for female and male components of fitness, and (3) whether the components of male and female reproductive success are equally affected by environmental factors. Some studies have documented genetic variation in both male and female functions, and evidence for a male–female trade-off was found in *Collinsia parviflora* when flower size was controlled for (Parachnowitsch and Elle 2004) although other studies have found no consistent pattern of such trade-offs (e.g., Schlichting and Devlin 1992, Mutikainen and Delph 1996, Strauss et al. 1996). A survey on the consequences of herbivory on male and female functions shows that these are neither equal nor proportional (Mutikainen and Delph 1996, Thomson et al. 2004), although we still need more data that evaluate the plastic responses of male and female components to different environmental factors. Studies on functional architecture are also necessary to estimate the genetic and phenotypic correlations between both quantitative and qualitative aspects of male and female functions.

ROLE OF POLLINATORS ON THE EVOLUTION OF FLORAL TRAITS AND DISPLAY

The evolution of plant mating systems has undoubtedly been linked to the evolution of traits that influence the type of pollination (animal vs. wind pollination) and pollinator attraction to flowers (e.g., quantity and quality of floral rewards, petal coloration, flower size, flowering time). By producing large floral displays, or great amounts of nectar, for instance, plants can affect the behavior of pollinators, which in turn influences gene flow among plants and, ultimately, plant fitness (see reviews in Zimmerman 1988 and Pellmyr 2002). The goal of numerous studies on pollination biology has been to identify pollination syndromes, that is, suites of structural and functional floral traits that presumably reflect adaptations to different types of pollinating agents (Proctor and Yeo 1973, Faegri and van der Pijl 1979, Hingston and McQuillan 2000, Wilson et al. 2004). The variation in floral characters within a species, and its association with the variation in reproductive success, has so far received less attention. Several studies have demonstrated phenotypic selection on floral traits (Galen 1989, Schemske and Horvitz 1989, Herrera 1993, Johnson and Steiner 1997, Hansen et al. 2000, Medel et al. 2003), whereas others have found no evidence of the fact that floral differences are the outcome of adaptation to pollinators (Herrera 1996, Wilson and Thomson 1996, Armbruster 2002). Some floral characters may not represent adaptations to current pollinators, but exaptations (Gould and Vrba 1982, Lamborn and Ollerton 2000), evolved as a consequence of selection by pollinators that are now extinct or not present in the current scenario. Studies of correlated trait shifts represent another way to reveal how frequently pollinators exert selection pressures on floral characters in nature, but have to be combined with experiments on the adaptive basis of the traits (e.g., Lamborn and Ollerton 2000, Tadey and Aizen 2001, Castellanos et al. 2003). In a review on pollination syndromes, Fenster et al. (2004) summarized studies of correlated phylogenetic and ecotypic shifts in flower traits and functional groups of pollinators (phylogenetic shifts implying that closely related plant species show different traits and rely on different functional groups of pollinators, and ecotypic shifts implying a correlation between variation in floral trait and pollinators within a species). More than 50% of the studies of the traits reward, morphology, and color had detected a correlated trait change, whereas less than 50% of the studies of the trait fragrance had detected a correlated change.

To determine the contribution of a pollinator to plant fitness (i.e., the pollinator effectiveness), it is essential (1) to quantify the number of flowers it pollinates (quantitative component) and (2) to evaluate its efficiency as a pollinator (qualitative component). The former depends on the frequency of pollinator visits to a plant and on the flower visitation rate whereas the latter is a function of the pollen delivered to stigmas, the foraging patterns, and the selection of floral sexual stage by the pollinator (Herrera 1988). Pollination effectiveness is determined by the product of (1) frequency of visitation and (2) efficiency, and somewhat counterintuitive there is not always a positive correlation between these two factors (e.g., Herrera 1988, Schemske and Horvitz 1989, Pellmyr and Thompson 1996, Gómez and Zamora 1999, Mayfield et al. 2001). However, such a positive correlation has been found (Olsen 1997, Fenster and Dudash 2001), and Vázquez et al. (2005) have developed a model that shows that the most frequent mutualists often contribute most to reproduction regardless of their efficiency on a per-interaction basis.

The strength of selection of floral traits by pollinators and the plant's response to such selection may be limited by factors that are either intrinsic (genetic or life history) or extrinsic (environmental) to the plant (Herrera 1996, 2005). Among the latter, the spatio-temporal variation in the composition of pollinator assemblages and in their relative abundance is probably the most important factor precluding or strongly reducing selection on floral traits by pollinators. Differences at a spatial and at a temporal scale in the assemblage of pollinators

have been frequently documented (Herrera 1995, Traveset and Sáez 1997, Gómez and Zamora 1999, Maad 2000, Thompson 2001, Eckert 2002a, Minckley et al. 1999), but see Cane et al. (2005) for a high similarity in pollinator assemblage over time. Such spatial and temporal differences can create a mosaic of selective regimes (Thompson 2005), and if the mosaic is at a small scale, for example, within the same geographical area where there is gene flow among plants, selection on floral traits is probably much weakened. Large variation has been found in the pollinator assemblage visiting *Lavandula latifolia* in southeastern Iberian Peninsula, both between individuals within a single population and among populations (Herrera 2005). Abiotic conditions such as shade and vicinity to streams accounted for much of the observed variation and were positively related to pollinator diversity, as expected in a dry Mediterranean habitat. Selection on floral traits may also be weakened if the effect of a specific pollinator is context dependent, as in the case of *Penstemons* where bees are less-effective pollinators than hummingbirds, so in the presence of the latter, traits attracting bees are selected against (Wilson et al. 2006). In *Ipomopsis agregata*, the presence of another plant species nearby increases competition for pollinators and affects selection on floral traits (Caruso 2000).

To date, most studies of evolution of floral traits have, explicitly or implicitly, been founded on an assumption of the most effective pollinator principle (Stebbins 1970), that is, that the most effective pollinators are driving the evolution of floral traits. An alternative view is that floral traits must not represent adaptations to the most common or the most effective pollinators as long as the trait provides a marginal increase in fitness (Aigner 2006). We should then expect to find adaptations to rare or inefficient pollinators as long as those adaptations do not reduce the effectiveness of common pollinators. This view is supported by the observation that many species tend to be pollinated by several types of pollinators despite very specialized floral traits (Ollerton 1996), and that the unexpected pollinators—given the pollination syndrome—may even be the most effective, as in the case of bumblebees that are five times more effective than hummingbirds in pollinating the hummingbird flower *Ipomopsis aggregata* (Mayfield et al. 2001).

Even if phenotypic selection on a floral trait occurs, it may have a small effect on individual variation in maternal fitness relative to that of other factors, such as plant size, herbivory, and seed dispersal success. For instance, individual variation in floral morphology of different species (*Calathea ovandensis* (Schemske and Horvitz 1989), *Viola cazorlensis* (Herrera 1993), and *Hormathophylla spinosa* (Gómez and Zamora 2000)) accounted for less than 10% of the variance in fruit production, and in a combined pollination and herbivore experiment the presence of pollinators had a positive effect on recruitment only when herbivores of flowers and fruits were absent (Herrera et al. 2002). As mentioned in the previous section, however, selection may occur via the male function, and thus it is necessary to examine both female and male fitness to determine if phenotypic selection is important (e.g., Primack and Kang 1989, Conner et al. 1996, Maad and Alexandersson 2004, Caruso et al. 2005). In species that produce more than one flower, the operational unit of either male or female function—when determining the effect of phenotypic selection of a floral trait on maternal fitness—has to be the whole floral display because, as mentioned earlier, the level of geitonogamy determines the incidence of self-pollination and pollen discounting, and ultim-ately the plant's mating success (Harder and Barrett 1996).

Reproductive assurance, that is, an increase in autonomous self-pollination when pollin-ators are rare or absent (Harder and Barrett 1996), has been shown both for populations (Fausto et al. 2001, Kalisz et al. 2004) and single flowers (Kalisz and Vogler 2003). Even if common, pollinators may also affect the levels of selfing, and thus offspring quality, by their inefficiency (Harder and Barrett 1996). For instance, they may move frequently among different plant species transporting pollen between them so that fertilization by conspecific pollen is interfered with (e.g., Thomson et al. 1981, Harder et al. 1993, Caruso and Alfaro 2000,

Brown et al. 2002) and pollen is lost on foreign stigmas (Campbell 1985, Feinsinger and Tiebout 1991). Pollinators may also be inefficient by making several visits to the same plant individual and thus promoting geitonogamy (e.g., Brunet and Sweet 2006). Although pollen limitation has been frequently demonstrated (reviewed in Ashman et al. 2004, Knight et al. 2005), only a few studies have investigated its consequences for progeny fitness in the field (Brown and Kephart 1999, Colling et al. 2004) and the exploration of effects on population persistence has only begun (Ashman et al. 2004).

During the last decade, there has been a debate over the degree of generalizations versus specialization in pollination systems (Waser et al. 1996, Johnson and Steiner 2000, Ollerton and Cranmer 2002, Vázquez and Aizen 2003, Fenster et al. 2004, Herrera 2005, Waser and Ollerton 2006). The classical view that pollination systems tend toward specialization and that pollinator specialization is critical to plant speciation has been implicit in many pollination studies (Grant 1949, Baker 1963, Grant and Grant 1965, Stebbins 1970, Crepet 1983), but was questioned by Waser et al. (1996) who argued that pollination systems are more generalized and dynamic than previously believed. Supporting this view is, for example, the rareness of a complete match of geographical ranges of plants and pollinators indicating nonobligate interactions (Thompson 2005) and the invasion of new areas by pollinators (references in Traveset and Richarson 2006). The conclusions about the prevailing generalization level in a system may to some extent be a question of definition, and can change depending on how pollinator generalization is measured. One can, for example, use raw counts of the number of pollinators, or consider the phyletic or functional diversity of them and estimate the fraction of pollinators used of the total available species pool (Gómez and Zamora 2006). A striking example of the importance of the method is a plant–pollinator system in Illinois (Robertson 1928), which has been defined both as generalized (Waser et al. 1996) and specialized (Fenster et al. 2004), depending on the classification of pollinators. The interest in degree of generalization of pollination systems has emphasized the importance of investigating whole pollination networks, that is, all interactions between plants and pollinating animals in a system (Memmot 1999, Olesen and Jordano 2002, Bascompte et al. 2003). One conclusion from such studies is that reciprocal specializations, that is, when a pollinator species and a plant species are exclusively interacting with each other, are rare in plant–pollinator systems (Minckley and Roulston 2006). Rather it seems that plant–pollinator interactions often are asymmetric so that specialized species often interact with generalist species (Bascompte et al. 2003, Vázquez and Aizen 2004). The concept of pollination syndrome, in fact, has sometimes proven to be of little use when predicting the pollinators of a certain plant species and when explaining interspecific variation in pollinator composition (Herrera 1996 and references therein; Ollerton and Watts 2000, Mayfield et al. 2001). In habitats where pollinators are uncommon, it is not rare to find plants with both abiotic and biotic pollinating agents (e.g., Gómez and Zamora 1996, Lázaro and Traveset 2005). Future studies that examine the spatio-temporal variation in pollinator assemblages and in pollen limitation (Dudash and Fenster 1997, Kay and Schemske 2004, Knight et al. 2005 and references therein) and which assess not only one but several of the interactions an organism experiences (Irwin 2006) are crucial to determine how often and in what conditions plants specialize to particular pollinator agents.

INFLUENCE OF BIOTIC POLLINATION IN ANGIOSPERM DIVERSIFICATION

A long-standing question in the study of plant evolution is how and to what extent the emergence of animal pollination has driven the great and rapid early speciation of flowering plants. Different authors (e.g., Raven 1977, Regal 1977, Burger 1981, Crepet et al. 1991, Eriksson and Bremer 1992) have argued that animal pollinators, referring mostly to insects, may have influenced the rate of angiosperm diversification by (1) promoting genetic isolation

of plant populations, through mechanical or ethological mechanisms (see review in Grant 1994), (2) promoting outcrossing, so genetically diverse populations may undergo rapid phyletic evolution, and (3) reducing extinction rates, as they move pollen across long distances among sparse populations. Similarly, it has been suggested that the biotic dispersal of seeds, mainly referring to dispersal by vertebrates, also has contributed to some extent to angiosperm diversification (e.g., Tiffney and Mazer 1995 and references therein, Smith 2001). However, there is still controversy whether animal pollination increases speciation, and using phylogenetic data recent studies have found both a decrease in speciation in wind-dispersed species (Dodd et al. 1999) as well as no evidence for species richness to be higher in animal-pollinated than in wind-pollinated groups (Bolmgren et al. 2003). It is also important to note that lineages other than the angiosperms, such as Gnetales, Benettitales, Cheirolepidiaceae, and Medullosales, were insect pollinated but never underwent species radiations (Gorelick 2001), and that numerous shifts in diversification rates have taken place within the angiosperms, and some quite recently, as shown by the construction of a supertree of all angiosperm families (Davies et al. 2004). In contrast to the view that biotic dispersal of pollen and seeds has caused or favored the speciation of angiosperms, other authors (e.g., Midgley and Bond 1991, Stebbins 1981, Doyle and Donoghue 1993, Ricklefs and Renner 1994) believe that morphological and physiological characters in flowering plants have played a more important role in their diversification, although both biotic and abiotic mechanisms may be acting simultaneously (Verdú 2002). The reason why angiosperms have been more successful than gymnosperms may lie more on factors such as the greater plasticity in (1) growth forms, (2) type of habitats they can inhabit, (3) ways to exploit the environmental resources, (4) types of reproduction (vegetative reproduction is very rare in gymnosperms), and (5) possibly even in types of breeding system, which is usually less complex in gymnosperms. As Ricklefs and Renner (1994) point out, however, it is important to consider that factors affecting the displacement of gymnosperms by angiosperms may not be the same as those affecting their diversification rate. Angiosperms may be competitively superior for different causes: efficiency of water use in particular dry environments, efficiency of insect pollination in habitats where wind is nearly or totally absent, rapid growth, double fertilization, capacity of vegetative reproduction, and so on. It is plausible, though, that angiosperm diversification has promoted their proliferation in some habitats and under some circumstances (by their diversity, angiosperms may be more likely to survive and propagate after an environmental stress such as a period of drought, which may be devastating for a species of gymnosperm). Ricklefs and Renner concluded that the major factor contributing to speciation is probably the capacity of taxa to exploit a wide range of ecological opportunities by adopting different growth forms and life histories and by differentiating morphologically to be pollinated and dispersed by different vectors (biotic and abiotic). The study by Tiffney and Mazer (1995), in contrast, does show an important effect of biotic dispersal of seeds in angiosperm diversification (they do not include pollination systems in their analysis). The reason for such conflicting results is attributed, by these two authors, to the pooling of angiosperms with different growth forms or other traits, which masks differences among various groups. They perform separate analyses for woody and herbaceous monocots and dicots, finding that dispersal by vertebrates contributes to species richness in woody dicots, and that abiotically dispersed families exhibit higher levels of diversification in herbaceous monocots and dicots than vertebrate-dispersed families. The possibility exists, therefore, that the effect of biotic dispersal of both pollen and seeds was underestimated in the analyses of Ricklefs and Renner. Other potential problems with this kind of analyses, pointed out by Bawa (1995), are (1) the use of families, rather than genera or species, as independent units and (2) the broad classification of pollination and seed dispersal into biotic and abiotic categories, as both categories are very heterogeneous. Further analyses that include more variables that might influence diversification (capacity of asexual reproduction, size of

flower, fruit and seed, specificity of pollinators, etc.) will certainly reveal new patterns and probably contribute to explain a larger fraction of the variation in species richness among taxa.

With the information gathered to date, most ecologists believe that insect pollination has relevantly contributed to the diversification of some of the most speciose families (e.g., orchids), but we need much more data to determine its role on the massive mid-Cretaceous angiosperm diversification (Crane et al. 1995). We also know that insect pollination was already present when angiosperms originated (early Cretaceous, about 130 and 90 million years ago), as shown by Jurassic fossils of Bennetitales, the closest fossil group to angiosperms, which suggest the presence of a plant–pollinator interaction (Crepet et al. 1991). The androecium in early angiosperms probably served as the only reward for insects, as it occurred in the Bennetitales, and flowers were presumably small, apetalous, with few structures, either asymmetric or cyclically arranged (Crepet et al. 1991). Such early flowers co-occurred with a greater variety of insects than previously thought. According to these authors, the idea that Coleoptera were the main early pollinators needs to be reviewed, as other insect groups (e.g., pollen-chewing flies and micropterygid moths) were also present at that time. Nectaries appeared later, and were present in many of the late Cretaceous rosids, when a rapid radiation of bees took place (Crepet et al. 1991). The Cretacean radiation of major pollinator groups such as bees, pollen wasps, brachyceran flies, and butterflies coincided with the appearance of entomophilous syndromes in Cretacean flowers (Grimaldi 1999). Similarly, the radiation of Lepidoptera coincides with patterns of accelerating radiation in angiosperms (Pellmyr 1992). However, there is still very little knowledge about the causes and effects of these events, and even though there exists a reliable phylogeny and information on pollinator function for Lepidoptera, Pellmyr (1992) found no evidence that the evolution of this group of insects caused radiation in flowering plants.

CONCLUDING REMARKS

To understand the evolutionary dynamics of plant reproduction, a unified approach between the study of (1) mating systems and (2) pollination biology is crucial. The study of factors that influence pollen transfer (floral morphology, timing of self- vs. outcross pollination, pollinator's effectiveness, etc.) gives valuable information to faithfully model the pollen movement within and among flowers, which reflect the outcome of various plant–pollinator interactions. Such modeling certainly helps to understand and compare the evolutionary dynamics in different pollination systems. The growing DNA sequence data help to assess the consequences of selfing and outcrossing on genetic variability within and between populations, and we need more information on how often evolutionary stability of mixed mating systems occurs in nature. More studies designed to detect natural and sexual selection on floral traits and display will allow determining the frequency of occurrence of floral adaptations to pollinators. In addition, further experimental studies of the relationships between flower traits, environmental variables, and mating systems are needed if we are to discern if a character is a cause or an evolutionary consequence of the breeding system. More data on whole pollinator assemblages visiting a plant species, and their spatio-temporal variation in composition and effectiveness, also permit evaluation of the degree of plant specialization to pollinators and knowledge of the extent to which biotic pollination may influence angiosperm diversification. The latter will be assessed as more reliable phylogenetic trees of plants and pollinators are built with both morphological and genetic data, and as more information on the other factors affecting diversification are available.

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