

Reproductive assurance through autogamous self-pollination across diverse sexual and breeding systems

K. R. Shivanna*

Ashoka Trust for Research in Ecology and the Environment, Royal Enclave, Srirampura, Jakkur Post, Bengaluru 560 064, India

Pollination becomes a constraint when conspecific plants and/or their pollinators become scarce. Many plant species have evolved autogamous self-pollination as a means of reproductive assurance (RA) under pollination-uncertain environments. So far RA has been studied and discussed largely with reference to self-compatible species producing bisexual flowers. RA seems to have evolved across all other sexual and breeding systems – monoecy, dioecy and self-incompatibility (SI). Both monoecy and dioecy produce bisexual flowers (andro/gyno-monoecy, andro/gynodioecy and polygamous conditions) which may provide RA. Similarly, most of the SI species are leaky and do set some seeds upon self-pollination. This phenomenon termed ‘partial self-compatibility’ is quite common and does provide RA in SI species. Although dioecy and SI have evolved as obligate outbreeding systems, they seem to have reached an evolutionary dead end because of the constraints for outcross pollination. In the light of habitat destruction leading to a reduction in the diversity and density of native pollinators, it is likely that many of the obligate outbreeders tend to shift to mixed mating system in the coming decades. Similarly, obligate mutualism in which each plant species is dependent on one animal species for pollination also seems to have reached a dead end and the trend is to abandon such obligate mutualism as a survival strategy. In the absence of such a change, obligate outbreeders and those with highly specialized pollination system are likely to become endangered or even extinct.

Keywords: Autogamy, dioecy, evolutionary dead end, mixed mating system, monoecy, reproductive assurance, self-incompatibility.

SUCCESSFUL reproduction is one of the key requirements for the stability of populations and their spread. Although flowering plants may reproduce through vegetative propagules as well as seeds, it is the latter that facilitates genetic recombination and permits evolutionary adaptations. Reproductive success through seeds depends on completion of a series of sequential events, beginning with

the development of functional pollen grains and ovules, and terminating in seed development. Pollination, deposition of the pollen grains from the anther onto the stigma, is one of the most critical requirements and determines, to a large extent, reproductive success of the species. As plants are stationary, they have to depend on external agents for pollination services. Nearly 90% of the plants depend on animals for pollination and the remaining on wind or water¹. Pollination success depends not only on the number but also the type of pollen grains deposited on the stigma. This number has to be adequate to initiate fruit development and pollen grains have to be of compatible type (conspecific pollen and outcross pollen in self-incompatible species).

The type of pollination that prevails in a population depends on the sexuality of the flower, its structure and the prevailing pollination environment, particularly the density of conspecific plants and of pollinators. The flower may be bisexual producing functional pollen grains and ovules, or male producing only functional pollen grains, or female producing only functional ovules. However, the sexuality of the plants/populations shows wider variations depending on the distribution of the male, female and bisexual flowers (Table 1).

Pollination may be autogamous (pollen coming from the same flower) or geitonogamous (pollen coming from

Table 1. Sexuality of plants and populations

| | |
|---------------------|---|
| Hermaphrodite: | Each plant bears only bisexual flowers. |
| Monoecious: | Each plant bears male and female flowers. |
| Andromonoecious: | Each plant bears male and bisexual flowers. |
| Gynomonoecious: | Each plant bears female and bisexual flowers. |
| Polygamomonoecious: | Each plant bears male, female and bisexual flowers; more commonly, most of the plants bear male and female flowers, but some plants produce a small proportion of bisexual flowers as well*. |
| Dioecious: | Each plant bears either male or female flowers. |
| Androdioecious: | Each plant bears either male or bisexual flowers. |
| Gynodioecious: | Each plant bears either female or bisexual flowers. |
| Polygamodioecious: | Each plant bears male or female or bisexual flowers; more commonly, apart from male and female plants, some plants produce a small proportion of flowers of opposite sex (males producing some female flowers or females producing some male flowers) and/or bisexual flowers*. |

*e-mail: shivanna@atree.org

*Often these conditions are referred to as polygamous.

other flowers of the same plant) or xenogamous (pollen coming from another non-clonal plant). The type of pollen deposited on the stigma determines genetic heterogeneity of the population. Autogamy and geitonogamy lead to homozygosity in the population. Although such populations thrive and spread in favourable habitats, they suffer inbreeding depression because of the accumulation of lethal alleles in the population². Repeated selfing, however, results in purging of deleterious recessive alleles thereby avoiding inbreeding depression. More importantly, inbred populations lose their ability to adapt to changing environment. Thus, inbreeding is not conducive for evolutionary potential of the species. Plants have evolved a number of devices to encourage outbreeding and discourage inbreeding. Herkogamy (location of the anthers and stigma at different levels) and dichogamy (temporal separation of pollen release and stigma receptivity) are common in species producing bisexual flowers. Dichogamous flowers may be protogynous (stigma becomes receptive before pollen release) or protandrous (pollen grains released before the stigma becomes receptive). Although herkogamy and dichogamy prevent autogamy, they are not effective in preventing geitonogamy, as pollen from other flowers which are in the male phase may get deposited on the receptive stigma of another flower of the same plant. This is true in monoecy also (Table 1). Geitonogamy is frequent in species which produce a large number of functional flowers at any given time, particularly in tree species. In many of the species the seeds are produced by self- as well as outcross-pollen, although the proportion of each may vary; this type of mating system is termed mixed mating^{3,4}. However, xenogamy is obligate in strictly self-incompatible (inability of plants producing bisexual flowers to set seeds upon self-pollination) and dioecious species (Table 1).

Although evolution of cross-pollination is the ideal strategy to maintain heterozygosity of the populations, it has serious limitations. Pollination often becomes a constraint either in the number or type of pollen deposited. Pollination limitation is quite common under diverse sexual systems and habitats⁵⁻⁹, and is largely the result of scarcity of conspecific plants or pollinators. This is frequent particularly in tropical tree species as the individuals are sparsely distributed in the forests, limiting outcross pollination. This reduces, proportionately, the number of fruits and seeds and thus affects reproductive success of the plant; such species may even experience reproductive failure. Pollination failure acts as a selection pressure and often drives plants to evolve effective methods to achieve some seed set even under uncertain pollination environments as a means of reproductive assurance (RA). Thus, evolution of reproductive system operates under conflicting pressures – the need to achieve outcross pollination to maintain genetic heterogeneity of the population and the need to achieve some seed set even under pollination constraints as a means of RA. The extent of realization

of these conflicting demands depends on a number of factors: sexuality of the species, the breeding system and the pollination environment.

Seed production through autogamous self-pollination under pollination constraints is the most common method of RA^{3,8}. Self-pollination is considered to be a derived condition from outcrossing and is one of the frequently evolved features in flowering plants⁸⁻¹¹. The extent of reproductive assurance varies greatly between species and populations. Many investigators consider seed set through apomixis and vegetative propagation as other means of RA⁸. Here the discussion is confined only to RA through autogamous self-pollination.

In the absence of some means of RA, species with monoecious, dioecious and strictly self-incompatible sexual systems suffer reproductive constraint/failure under unreliable pollination environments. So far RA has generally been discussed with reference to species with bisexual, self-compatible reproductive systems^{8,9,11-18}. However, species with specialized sexual and breeding systems (monoecy, dioecy and self-incompatibility) have also evolved RA to some extent. This review examines RA through autogamy across diverse sexual and breeding systems in flowering plants and emphasizes the need for the evolution of RA as a survival strategy in specialized systems.

Bisexual, self-compatible systems

Spontaneous autogamy can occur only in bisexual flowers. The basic requirements for autogamous pollination are: positioning of the anthers and the stigma close to each other so that the dehiscent anthers come in contact with the stigma, overlapping of pollen dispersal and stigma receptivity, and self-compatible breeding system. Autogamous selfing may occur at different times during the life span of the flower: prior selfing before the flower gets any opportunity for outcrossing, competing selfing when the flower has equal opportunity for selfing as well as outcrossing and delayed selfing toward the end of the life span after all opportunities for outcrossing are over.

Cleistogamous flowers

Cleistogamous flowers do not open and thus the stamens and pistil remain enclosed within the flower bud. Cleistogamy has been reported to occur in 693 species from 228 genera and 50 families¹⁹. All the requirements for autogamy are fully met in cleistogamous flowers. The anthers and stigma are in close proximity to each other^{2,19-21}. Pollen grains germinate inside the anther or after coming in contact with the stigma following anther dehiscence; pollen tubes enter the stigma and grow through the pistil and release sperm cells in the embryo sac for fertilization. Thus, cleistogamous flowers are exclusively autogamous.

Most of the cleistogamous species, however, produce both cleistogamous and chasmogamous (that open) flowers. Often the production of cleistogamous flowers depends on the prevailing environmental conditions, particularly the temperature and light. Cleistogamous flowers provide RA through autogamy in these species and chasmogamous flowers permit outcross pollination. Thus cleistogamous species tend to show mixed mating strategy (discussed later).

Chasmogamous flowers

Chasmogamous flowers invariably open and facilitate pollen dispersal and receipt of outcross pollen. In zoophilous species, flowers generally offer pollen and/or nectar as rewards to attract floral visitors^{22,23}. Extensive studies have been carried out on RA through autogamy in chasmogamous flowers^{8,9,12,24}. RA results in fitness gains to the species in several ways^{2,8,9,15,25–27}. RA enables populations to colonize, reproduce and spread even under severe pollination constraints. It facilitates the species to exploit dormancy and dispersal related advantages of seeds to establish populations away from the parent plant, irrespective of the number of individuals in the new population, and presence or absence of pollinators. For an autogamous species, dispersal of a single seed is sufficient to establish a sexually reproducing new population, but for a nonautogamous species a minimum of two seeds is needed to establish a population, provided both the resulting plants grow close (spatially and temporally) to each other and an effective pollinator is present. Autogamous individuals also escape competition for pollinators. A number of investigations have shown that the sexual systems are labile and populations may shift rapidly toward autogamy by changing floral traits under conditions of pollination limitation and environmental stresses^{8,27}.

Since long the role of RA has been emphasized for colonization success of weed species in new locations^{25–28}. RA is particularly critical in annual weeds as they lack vegetative reproduction and get only one opportunity to set seeds in their life; if they miss this opportunity, their survival and spread is threatened. As far as pollination strategies are concerned, biennials are similar to annuals as they also flower only once in their life. Perennial weeds, on the other hand, generally have dual strategy for reproduction, through seeds as well as vegetative propagules and also get repeated opportunities for seed set. Survival and fitness of perennial weeds, therefore, are not seriously threatened even if they do not produce seeds in some years. In agreement with this hypothesis, all the 23 annual weed species of Canada tested have been reported to be capable of setting viable seeds in bagged flowers²⁹. On the other hand, none of the eight rhizomatous and stoloniferous perennial weed species tested set seeds in bagged flowers²⁹, indicating absence of RA in such

perennial weeds. Recent studies on pollination strategies of 15 annual weed species of India also showed a high level of autogamy in all the species and there was no difference in the extent of seed set between bagged and open-pollinated flowers¹⁶. However, the breeding system of perennial weed species is similar to non-weedy species; some do show RA through autogamy and others are dependent on pollinating agents for effective pollination¹⁸.

Obligate outbreeding systems

Monoecy

Monoecy in which both male and female flowers are present on the same individual, is generally considered to be a derived condition from bisexual system and also as one of the pathways for the evolution of dioecy. The frequency of monoecy varies from 3% to 19% in different ecological conditions, the highest being in tropical forests³⁰. Monoecy is less intensively investigated when compared to dioecy.

Monoecy has been suggested to provide many advantages to the species³¹. Some of the advantages are that it favours outcrossing, reduces pollen–stigma interference and allows a more flexible allocation of gender in a variable environment. As pointed out earlier, monoecy is effective in preventing autogamous selfing, but not geitonogamous selfing. Monoecy is as common in self-incompatible species as in self-compatible ones, thus raising doubts on the role of monoecy as an outbreeding mechanism³². There are evidences to indicate that monoecy provides a mechanism to modulate resource allocation to male and female functions by varying the proportion of pistillate and staminate flowers in response to resource availability^{33,34}. In several species the proportion of male and female flowers has been shown to be plastic and vary in response to the extent of fruit development^{35–37}. For example, in *Solanum hirtum* plants bearing fruits produce a greater proportion of staminate flowers than those in which fruit production is limited³⁵; this would enable the plant to divert resources to the development of staminate flowers as continued fruit production becomes resource-limited.

Many monoecious species show andromonoecious, gynomoecious or polygamomoecious (Table 1) condition and produce a proportion of bisexual flowers on such plants. Both andro- and gyno-monoecy are quite common and are considered to occur in response to pollination limitation and environmental stresses³⁸. Andromonoecy occurs in about 4000 species of flowering plants from over 33 families and has evolved independently in numerous plant lineages³⁷. Gynomoecy has been estimated to occur in 2.8% of flowering plants³⁹ belonging to about 23 families⁴⁰. Sexual expression in andromonoecious^{35,37} and gynomoecious⁴¹ plants is generally plastic; the proportion

of unisexual flowers varies depending on the extent of fruit development³⁸.

Although the occurrence and extent of self-pollination in bisexual flowers in andromonoecious, gynomonoecious and polygamomonoecious plants have not received much attention by pollination biologists, they are likely to provide reproductive assurance through autogamous self-pollination. For example, in *Silene noctiflora*, a gynomonoecious species, bisexual flowers have been reported to be capable of autogamous selfing and thus provide RA⁴¹. Prior autogamy in the bud stage resulted in fertilization of 45% of the ovules and autogamy continued even after flower opening and reached up to 95%. There was no difference in the extent of seed set in bisexual flowers between bagged flowers and those open to pollinators. Seed set in emasculated (but unbagged) flowers was very low indicating that RA through selfing is an important trait of bisexual flowers in this species and may have been selected under pollination constraints. Therefore, RA, can be considered as an additional evolutionary advantage of andro-, gyno- and polygamo-monoecy.

Dioecy

Dioecy is a sexual system in which male and female flowers are produced on separate individuals. Although several pathways have been suggested for the evolution of dioecy, many investigators support its evolution from cosexuality via gynodioecy or monoecy. Dioecy has evolved polyphyletically in different lineages and evolutionary pathways of dioecy have been elaborated by a number of evolutionary biologists^{4,42-47}. According to the latest estimate⁴⁸ there are 15,600 dioecious species belonging to 987 genera and 175 families; this works out to be 5–6% of the species, 7% of the genera and 43% of the families. Dioecy has been associated with spatial distribution of plants such as tropical forests and oceanic islands, stressful environments, life span of the species, ecological features such as woodiness and climbing habit and species with generalized entomophilous pollination⁴⁹⁻⁵¹. In tropical species it is reported to be about 15% (refs 49–53). In a sandy coastal vegetation of Brazil, a high proportion of dioecy in woody species (35%) has been reported⁵³.

Dioecy has been an area of intensive studies since 1930s. The evolution of dioecy is considered to be an adaptation to prevent inbreeding, although in some species selection for sexual specialization leading to accelerated fitness may also have led to the origin of dioecy^{43,54}. However, this does not appear to be a general feature as most dioecious species have close cosexual relatives with some outbreeding features such as herkogamy, dichogamy, self-incompatibility or monoecy^{45,55}. Although the main advantage of dioecy is that all seeds produced are the result of outcross pollination, it carries many disadvan-

tages: it is prone to pollination limitation under pollinator-scarce environment, limitation of seed set only to about half the individuals (females) and difficulty in spreading to new areas as at least one male and one female are required in the new site for seed set.

In most dioecious species, sexuality seems to be labile; sexual intermediates and sexual switching are frequent⁴⁵. They show plasticity both temporally and spatially largely based on the prevailing environmental conditions^{2,48}. Temporal changes in the sexuality of dioecious species are not well documented when compared to spatial changes, as the former requires continuous monitoring of sexuality during the entire flowering period of the plant. In *Nothapodytes nimmoniana*, for example, several male individuals (<10%) start producing female and bisexual flowers towards the end of the flowering season leading to polygamous condition⁵⁶. Such temporal changes may not have been recorded in many of the dioecious species; further studies may reveal many more dioecious species to be sexually labile leading to the production of bisexual flowers.

Gynodioecy in which populations consist of separate male and hermaphrodite individuals has been reported in about 1.4% of angiosperm genera^{2,57}. It is considered to be an intermediate condition in the evolution from hermaphroditic to dioecious breeding system^{4,42,58,59}. Androdioecy in which populations consist of separate male and hermaphrodite individuals is rare and considered to have evolved from dioecy^{4,42,59,60}. Pollen limitation has been suggested to be the selective force for the evolution of androdioecy from dioecy⁶¹. Studies on species of *Acer*, however, indicate that dioecy has evolved from androdioecy⁶⁰.

There are hardly any critical studies on the possibility and extent of autogamy in bisexual flowers produced in gyno- and andro-dioecious or polygamous individuals. A majority of gynodioecious species are reported to be self-compatible^{62,63} indicating the possibility of autogamy in many such species. Crossman and Charlesworth⁶⁴ have suggested that breakdown of dioecy in the population is the result of pollen limitation leading to males becoming cosexual and self-fertile, thus providing RA. In *N. nimmoniana*, the bisexual flowers produced in polygamous individuals are self-compatible and set fruits under open pollination. Over 25% of the bagged bisexual flowers also set fruits confirming their ability to provide RA through autogamy⁵⁶.

Gynodioecy, androdioecy and polygamous conditions (which contain plants with bisexual flowers) may represent a stable sexual system rather than transitory stages in several species. They may also arise secondarily from dioecy to overcome pollination constraints. Additionally, these conditions may arise in response to ecological stresses as a result of sexual plasticity. Hermaphrodite flowers, in all these sexual systems, irrespective of their origin, if capable of autogamy, do provide RA to the population.

Self-incompatibility

In majority of the species, SI is controlled by multiple alleles at one locus termed $S_1, S_2, S_3, \dots, S_n$. When there is allelic matching between the pollen grains and the pistil, as it happens in self-pollinations, the pollen grains are inhibited during germination or pollen tube growth. SI is an important outbreeding mechanism and the information available on the structural and functional details and on the genetics of SI is enormous^{2,10,65}. Self-compatibility (SC) is considered to be the derived condition. Seed set in SC plants upon self-pollination is, as expected, as good as in cross-pollinated flowers. Transition from SI to SC is thought to be irreversible^{10,66}.

SI in most of the species is leaky and results in some seed set upon self-pollination, although the extent of seed set in selfed flowers is highly variable (from almost nil to slight preference for outcross-pollen); this is referred to as partial self-compatibility (PSC), partial self-incompatibility or pseudo-compatibility. Many investigators have estimated the index of SI (ISI) using the formula⁶⁷: ISI = extent of fruit set in self-pollinated flowers/extent of fruit set in cross-pollinated flowers. The extent of fruit set is assessed on the basis of either per cent fruit set or the mean number of seeds per fruit/pollination. The species is considered to be fully self-compatible when ISI is 1 or >1, partially self-compatible (PSC) when ISI is >0.2 but <1, and fully self-incompatible when ISI is <0.2 or 0. Thus PSC is a common feature amongst SI species. PSC was known since long⁶⁸ and has been reported in a large number of species. As more and more wild species are being investigated, examples of PSC are steadily increasing^{69,70}. Thus, SI is generally a plastic trait and the strength of SI varies amongst individuals⁷¹. Apart from genetic make-up of the individual, selfing rates can respond to pollinator constraints and environmental stresses such as high temperature^{10,65-72}.

Although PSC has been explained by some investigators as a transitional stage between SI and SC, the evidences do not support such a concept⁷³. On the basis of our understanding of the genetics and functioning of SI, a species/population is either SI or SC; there is no scope for PSC. Evolution of self-compatibility from SI individual is well recognized by non-functional S allele in the pollen and/or the pistil as a result of mutation¹⁰. The genetics of PSC is not clear. According to Vallejo-Marín and Uyenoyama⁶⁹, PSC is due to the action of alleles modifying the strength of SI alleles. PSC is maintained in the populations by complex interactions between the SI locus and those modifying the strength of SI. Thus, PSC is not a transitory condition between full SI and full SC, but a stable condition⁷³. The anthers and stigma in many of the homomorphic SI species such as *Petunia*, *Nicotiana* and *Brassica* are positioned close to each other to permit autogamy. Although the possibility of autogamy in PSC systems is not investigated in most of the species,

autogamous selfing is likely to occur at least to some extent in many of these SI species. Therefore, PSC can be considered as an important means of RA in SI species. Autogamy is unlikely to occur in heteromorphic species. This may be a reason for the evolution of only a limited number of heteromorphic SI species.

Low density of tree species in tropical forests acts as a serious limitation for outcross pollination. However, SI and dioecy, which require obligate cross-pollination are more prevalent in tropical forests^{6,50,51,74}. As wind is not an effective pollinator in tropical forests because of closed canopy, wind pollination is not a prevalent feature. Although the strength of SI in tropical forests is not well investigated, many of the SI species are reported to be PSC⁷⁰ and thus autogamous self-pollination is likely to provide RA in such species. This may explain the prevalence of SI in tropical forests.

Wind pollination

Wind pollination is considered to have evolved under scarce pollinator environment^{75,76}. Interestingly, wind pollination seems to have evolved more frequently in animal-pollinated lineages with unisexual flowers^{48,55,77-80}. Wind pollination is reported to be present in about 31.6% of dioecious species compared to about 6% of non-dioecious species. Many of the dioecious species that depend on biotic pollination exhibit low reproductive success and this may have acted as a selection pressure for the evolution of wind pollination^{52,81}. Unlike in hermaphrodite flowers, autonomous self-pollination cannot evolve in unisexual flowers to overcome pollinator constraints, but wind pollination is an effective alternative to relieve pollen limitation. Under pollinator-scarce environment, the possibilities of pollen deposition through wind are much higher. Even under scarcity of conspecific plants in the habitat, geitonogamous self-pollination can readily occur in wind-pollinated monoecious species. In fact, analysis of mating pattern based on genetic markers in seven monoecious *Carex* species has shown that geitonogamous self-pollinations predominate and thus provide RA under ecological conditions that limit outcross pollination⁷⁶. As pointed out by Friedman and Barrett⁷⁵, reproductive assurance has seldom been extended to cover wind-pollinated species. Apart from monoecious species, wind-mediated geitonogamy can also prevail in andro- and gyno-dioecious, and polygamous individuals and is likely to provide RA. Thus wind pollination in general, and monoecious and dioecious species in particular do provide RA in the absence of biotic pollinators.

Mixed mating system: effective compromise between inbreeding and outbreeding

Since the time of Darwin, the advantages of selfing in inbreeding populations are considered to be short-lived

owing to higher rates of extinction due to their reduced ability to adapt to environmental changes imposed by their increased homozygosity^{2,82}. Stebbins⁸² even considered obligately selfing species as an 'evolutionary dead end'. Many of the recent studies on pollination strategies are not entirely in agreement with this concept⁶⁶.

An important feature of most of the populations that show RA through autogamy is their ability to permit outcross pollination as and when the pollinators are available. Thus, selfing species tend to show mixed mating system to different degrees depending on the prevailing pollination environments^{73,83}. In fact, it has been argued that very few plant species, if any, show complete selfing⁶⁶. In several cases intermediate selfers have been reported to show the lowest extinction risk^{28,83}. Over 40% of the species, out of 345 species belonging to 75 families analysed for mating system, was found to show mixed mating system^{73,83}. Mixed mating system appears to be a stable mating system rather than transitory to full selfing⁸³. In the light of all these studies, mixed pollination appears to be the most successful mating strategy.

As pointed out earlier, the sexual system in most of the species is not absolute; it is plastic to different degrees based on genetic make-up and environmental stresses. Because of this plasticity, the populations show temporal and spatial variations in the extent of self and outcross pollinations²⁷. Many studies have shown that populations growing in the disturbed habitats and pollinator-poor environments show higher selfing rate than those growing in undisturbed and pollinator-rich habitats⁸. This flexibility in the mating system gives fitness gains and facilitates population stability. Further, changes in floral traits favouring autogamy under pollination constraints operate at local population level and not at the species level. Selfing rates in different populations within the same species may range from complete selfing to complete outcrossing⁴. Thus the negative effects of inbreeding seem to have been over-emphasized in the literature. Certainly there is much more to be learnt on the survival and evolutionary strategies of 'inbreeders'.

Another negative effect associated with predominantly selfing populations is the decline in diversification of species because of their inability to adapt to changing environment⁶⁶. However, as selfing facilitates local adaptations and changes in a number of floral traits, it enhances sympatric as well as allopatric isolation mechanisms⁸⁴⁻⁸⁸. These features act as reproductive isolation mechanisms resulting in reduced gene flow between populations leading to speciation⁸⁴. Based on theoretical considerations and studies on mating system evolution, Takebayashi and Merrell⁸⁹ concluded that 'it is premature to assess whether genetic variation is sufficiently reduced to eliminate adaptive potential and drive populations to extinction' in selfed species.

Are obligate outbreeders and specialized pollination systems evolutionary dead ends?

Adaptation to outbreeding has been the main emphasis in the evolution of sexual systems^{2,4}. Evolution of dioecy is the ultimate means of achieving obligate outcrossing^{4,42,55,90}. Although it has wide distribution at the family level (in about half of the families, including basal angiosperms), it is limited to only about 6% at the species level^{4,78}. Thus, dioecy does not seem to have become a successful mating system; dioecious lineages seem to have fewer species compared to their cosexual sister taxa⁹¹. This may be the result of reduced speciation rate and/or higher rate of extinction in dioecious taxa⁴. According to Richards² 'dioecy rarely seems to last long enough in evolutionary time, or to be successful enough to establish a dynasty'. It is quite possible that some of the species with gynodioecy and androdioecy represent reversal from dioecy as a result of selection pressure for reproductive assurance. Similarly, SI is another mating system that requires obligate outcrossing. Even this system does not seem to be successful. There seem to be few, if at all, strictly SI species; a majority of the SI species seem to have become self-compatible or partially self-compatible as a means of reproductive assurance.

Another focal theme on the evolution of pollination system since the time of Darwin has been from generalization (many pollinators) to specialization (limited number of pollinators)^{92,93}. However, many recent studies have shown that a large proportion of plant species have adopted a generalized pollination system^{94,95}. It is only in a limited number of species that the trend of specialization has resulted in obligate mutualism as a result of co-evolution; each plant species in such mutualism is pollinated by one specific pollinator^{96,97}. Classical examples cited in the literature for such a specialization are fig pollinated by fig wasps, and yucca pollinated by yucca moth. Such obligate specialization in which the pollinator and plant species are dependent on each other for sexual reproduction is prone for extinction when one of the partners becomes scarce/extinct⁹⁸. Many studies in recent years have shown that such obligate specializations are breaking down in some species of fig^{98,99} and yucca¹⁰⁰, and they seem to be evolving towards more generalized pollination system opting for additional pollinators⁹⁸⁻¹⁰⁰. Similarly, Orchidaceae is one of the largest families with highly specialized pollination syndromes. Deceptive pollination is prevalent in orchids; one-third of orchid species are reported to be deceptive. Sexual deception, present in several orchids, is highly specialized and each orchid species is pollinated by a species-specific pollinator. However, molecular data have shown that gene flow between sympatric sexually deceptive species is quite common, indicating breakdown of highly specialized pollination system¹⁰¹. Evolution of such features which provide reproductive assurances may have enabled this

family to thrive even under pollination limitation. The extent of autogamy is also quite high in orchids; about 30% of orchids in studied species are reported to be autogamous^{102,103}. Self-incompatibility is also rare in orchids; when present it is partially self-compatible^{104,105}. These studies clearly indicate that highly specialized pollination systems, similar to obligate outbreeding systems, are not successful and tend to change their mating pattern under conditions of pollinator scarcity as a survival strategy.

Concluding remarks

There has been a lot of concern in recent years on the effects of habitat degradation and climate change on the sustenance of our biodiversity. Several studies have shown that these anthropogenic perturbations have greatly reduced the density and diversity of pollinators^{9,106–109}. Parallel declines in specialized pollinators and plant species that depend on such pollinators have been highlighted¹⁰⁶. In the light of continued human disturbances in the coming years, we may expect evolution of floral traits more favourable for autogamy to various degrees even in predominantly outcrossed species as a survival strategy. This would lead to more and more species shifting to mixed mating system. Similarly, species with highly specialized pollination system with obligate mutualism are likely to evolve towards a more generalized system. Those species incapable of such shifts are likely to become extinct. Although considerable data are available on RA in bisexual self-compatible species, there is little information on specialized sexual systems. It is, therefore, important for pollination biologists to study the occurrence and extent of autogamy in such specialized systems to get a better idea about the sustenance of diverse sexual systems.

1. Ollerton, J., Winfree, R. and Tarrant, S., How many flowering plants are pollinated by animals? *Oikos*, 2011, **120**, 321–326.
2. Richards, A. J., *Plant Breeding Systems*, Allen and Unwin, London, 1986.
3. Cruden, R. W. and Lyon, D. L., Facultative xenogamy: examination of a mixed mating system. In *The Evolutionary Ecology of Plants* (eds Bock, J. H. and Linhart, Y. B.), Westview, Boulder, 1989, pp. 171–207.
4. Barrett, S. C. H., The evolution of plant sexual diversity. *Nat. Rev. Genet.*, 2002, **3**, 274–284.
5. Burd, M., Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Bot. Rev.*, 1994, **60**, 83–139.
6. Wilcock, C. and Neiland, R., Pollination failure in plants: why it happens and when it matters. *Trends Plant Sci.*, 2002, **7**, 270–277.
7. Knight, T. M. *et al.*, Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.*, 2005, **36**, 467–497.
8. Eckert, C. G., Samis, K. E. and Dart, S., Reproductive assurance and the evolution of uniparental reproduction in flowering plants. In *Ecology and Evolution of Flower* (eds Harder, L. D. and

- Barrett, S. C. H.), Oxford University Press, New York, 2006, pp. 183–203.
9. Eckert, C. G. *et al.*, Plant mating systems in a changing world. *Trends Ecol. Evol.*, 2010, **25**, 35–43.
10. de Nettancourt, D., *Incompatibility and Incongruity in Wild and Cultivated Plants*, Springer-Verlag, Berlin, 2001.
11. Levin, D. A., Mating system shifts on the trailing edge. *Ann. Bot.*, 2012, **109**, 613–620.
12. Wyatt, R., The evolution of self-pollination in granite outcrop species of *Arenaria* (Caryophyllaceae). 1. Morphological correlates. *Evolution*, 1984, **38**, 804–816.
13. Barrett, S. C. H. and Eckert, C., Variation and evolution of mating systems in seed plants. In *Biological Approaches and Evolutionary Trends in Plants* (ed. Kawano, S.), Academic Press, Tokyo, 1990, pp. 229–254.
14. Kalisz, S. and Vogler, D. W., Benefits of autonomous selfing under unpredictable pollinator environments. *Ecology*, 2003, **84**, 2928–2942.
15. Busch, J. W. and Delph, L. F., The relative importance of reproductive assurance and automatic selection as hypotheses for the evolution of self-fertilization. *Ann. Bot.*, 2012, **109**, 553–562.
16. Shivanna, K. R., Reproductive assurance through autogamy in some annual weed species. *Proc. Natl. Acad. Sci. India. Sect. B*, 2014, **84**, 681–687.
17. Shivanna, K. R., *Trichodesma zeylanicum* – a species with chasmogamous flowers but obligate autogamy. *Curr. Sci.*, 2014, **107**, 743–745.
18. Shivanna, K. R., Pollination strategies of some perennial weed species. *Proc. Indian Natl. Sci. Acad.*, 2015, **81**, 485–492.
19. Culley, T. M. and Klooster, M. R., The cleistogamous breeding system: a review of its frequency, evolution, and ecology in angiosperms. *Bot. Rev.*, 2007, **73**, 1–30.
20. Lord, E. M., Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. *Bot. Rev.*, 1981, **47**, 421–449.
21. Kaul, V. and Koul, A. K., Sex expression and breeding strategy in *Commelina benghalensis* L. *J. Biosci.*, 2009, **34**, 977–990.
22. Willmer, P., *Pollination and Floral Ecology*, Princeton Univ Press, Princeton, NJ, 2011.
23. Shivanna, K. R., Biotic pollination: how plants achieve conflicting demands of attraction and restriction of potential pollinators. In *Reproductive Biology of Plants* (eds Ramawat, K. G., Merillon, J.-M. and Shivanna, K. R.), CRC Press, Boca Raton, 2014, pp. 218–267.
24. Barrett, S. C. H., The reproductive biology and genetics of island plants. *Philos. Trans. R. Soc. London, Ser. B*, 1996, **351**, 725–733.
25. Baker, H. G., Self-compatibility and establishment after 'long distance' dispersal. *Evolution*, 1955, **9**, 347–348.
26. Baker, H. G., The evolution of weeds. *Annu. Rev. Ecol. Syst.*, 1974, **5**, 1–24.
27. Barrett, S. C. H., Why reproductive systems matter for the invasion biology of plants. Invasiveness may result in a change in community composition. In *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. (ed. Richardson, D. M.), Blackwell, Chichester, 2011, pp. 195–210.
28. Cheptou, P.-O., Clarifying Baker's law. *Ann. Bot.*, 2012, **109**, 633–641.
29. Mulligan, G. A. and Findlay, J. N., Reproductive systems and colonization in Canadian weeds. *Can. J. Bot.*, 1970, **48**, 859–860.
30. Machado, I. C., Lopes, A. V. and Sazima, M., Plant sexual systems and a review of the breeding systems in the Caatinga, a Brazilian tropical dry forest. *Ann. Bot.*, 2006, **97**, 277–287.
31. de Jong, T. J., Shmida, A. and Thuijisman, F., Sex allocation in plants and the evolution of monoecy. *Evol. Ecol. Res.*, 2008, **10**, 1087–1109.
32. Bertin, R. I., Incidence of monoecy and dichogamy in relation to self-fertilization in Angiosperms. *Am. J. Bot.*, 1993, **80**, 557–560.

33. Bertin, R. I., The evolution and maintenance of andromonoecy. *Evol. Theory*, 1982, **6**, 25–32.
34. Spalik, K., On the evolution of andromonoecy and ‘overproduction’ of flowers: a resource allocation model. *Biol. J. Linn. Soc.*, 1991, **42**, 325–336.
35. Diggle, P. K., Developmental plasticity, genetic variation, and the evolution of andromonoecy in *Solanum hirtum* (Solanaceae). *Am. J. Bot.*, 1993, **80**, 967–973.
36. Diggle, P. K., The expression of andromonoecy in *Solanum hirtum* (Solanaceae): phenotypic plasticity and ontogenetic contingency. *Am. J. Bot.*, 1994, **81**, 1354–1365.
37. Miller, J. S. and Diggle, P. K., Diversification of andromonoecy in *Solanum* section *Lasiocarpa* (Solanaceae): the roles of phenotypic plasticity and architecture. *Am. J. Bot.*, 2003, **90**, 1313–1320.
38. Ashman, T.-L., The evolution of separate sexes: a focus on the ecological context. In *Ecology and Evolution of Flowers*. (eds Harder, L. D. and Barrett, S. C. H.), Oxford University Press, New York, 2006, pp. 204–222.
39. Bertin, R. I. and Kerwin, M. A., Floral sex ratios and gynomoecy in Aster (Asteraceae). *Am. J. Bot.*, 1998, **85**, 235–244.
40. Mamut, J. and Tan, D.-Y., Gynomoecy in angiosperms: phylogeny, sex expression and evolutionary significance. *Chin. J. Plant Ecol.*, 2014, **38**, 76–90.
41. Davis, S. L. and Delph, L. F., Prior selfing and gynodioecy in *Silene noctifolia* L. (Caryophyllaceae): opportunities for enhanced outcrossing and reproductive assurance. *Int. J. Plant Sci.*, 2005, **166**, 475–480.
42. Charlesworth, B. and Charlesworth, D., A model for the evolution of dioecy and gynodioecy. *Am. Nat.*, 1978, **112**, 975–997.
43. Charlesworth, D. and Charlesworth, B., Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.*, 1987, **18**, 237–268.
44. Ross, M. D., Five evolutionary pathways to subdioecy. *Am. Nat.*, 1982, **119**, 297–318.
45. Freeman, D. C. *et al.*, Sexual specialization and inbreeding avoidance in the evolution of dioecy. *Bot. Rev.*, 1997, **63**, 65–92.
46. Jacobs, M. S. and Wade, M. J., A synthetic review of the theory of gynodioecy. *Am. Nat.*, 2003, **161**, 837–851.
47. Barrett, S. C. H. and Hough, J., Sexual dimorphism in flowering plants. *J. Exp. Bot.*, 2013, **64**, 67–82.
48. Renner, S. S., The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *Am. J. Bot.*, 2014, **101**, 1588–1596.
49. Bawa, K. S., Evolution of dioecy in flowering plants. *Annu. Rev. Ecol. Syst.*, 1980, **11**, 15–39.
50. Bawa, K. S. and Opler, P. A., Dioecism in tropical forest trees. *Evolution*, 1975, **29**, 167–179.
51. Bawa, K. S. *et al.*, Reproductive biology of tropical lowland rain forest trees. 2. Pollination systems. *Am. J. Bot.*, 1985, **72**, 346–356.
52. Matallana, G., Wendt, T., Araujo, D. S. D. and Scarano, F. R., High abundance of dioecious plants in a tropical coastal vegetation. *Am. J. Bot.*, 2005, **92**, 1513–1519.
53. Senarath, W. T. P. S. K., Dioecy and monoecy in the flora of Sri Lanka and their evolutionary correlations to endemism, growth form, fruit type, seed number and flower size. *Bangladesh J. Plant Taxon.*, 2008, **15**, 13–19.
54. Thomson, J. D. and Barrett, S. C. H., Selection for outcrossing, sexual selection, and the evolution of dioecy in plants. *Am. Nat.*, 1981, **118**, 443–449.
55. Givnish, T. J., Outcrossing versus ecological constraints in the evolution of dioecy. *Am. Nat.*, 1982, **119**, 849–865.
56. Sharma, M. V., Uma Shaanker, R., Vasudeva, R. and Shivanna, K. R., Functional dioecy in *Nothapodytes nimmoniana*, a distylous species in the Western Ghats. *Curr. Sci.*, 2010, **99**, 1444–1449.
57. McCauley, D. E. and Bailey, M. F. Recent advances in the study of gynodioecy: the interface of theory and empiricism. *Ann. Bot.*, 2009, **104**, 611–620.
58. Lloyd, D. G., The maintenance of gynodioecy and androdioecy in angiosperms. *Genetica*, 1975, **45**, 325–339.
59. Pannell, J. R., The evolution and maintenance of androdioecy. *Annu. Rev. Ecol. Syst.*, 2002, **33**, 397–425.
60. Gleiser, G. and Verdu, M., Repeated evolution of dioecy from androdioecy in *Acer*. *New Phytol.*, 2005, **165**, 633–640.
61. Wolf, D. E. and Takebayashi, N., Pollen limitation and the evolution of androdioecy from dioecy. *Am. Nat.*, 2004, **163**, 122–137.
62. Meagher, T. R., Linking the evolution of gender variation to floral development. *Ann. Bot.*, 2007, **100**, 165–176.
63. Ehlers, B. K. and Schierup, M. H., When gametophytic self-incompatibility meets gynodioecy. *Genet. Res. Cambridge*, 2008, **90**, 27–35.
64. Crossman, A. and Charlesworth, D., Breakdown of dioecy: models where males acquire cosexual function. *Evolution*, 2013, **68**, 426–440.
65. Shivanna, K. R., *Pollen Biology and Biotechnology*, Science Publishers, Enfield, USA (special Indian edition: Oxford-IBH Publishers, New Delhi), 2003.
66. Wright, S. I., Kalisz, S. and Slotte, T., Evolutionary consequence of self-fertilization in plants. *Proc. R. Soc. London, Ser. B*, 2013, **280**, <http://dx.doi.org/10.1098/rspb.2013.0133>
67. Zapata, T. R. and Arroyo, M. T. K., Plant reproductive ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica*, 1978, **10**, 221–230.
68. Brink, R. A. and Cooper, D. C., Partial self-incompatibility in *Medicago sativa*. *Proc. Natl. Acad. Sci. USA*, 1938, **24**, 497–499.
69. Vallejo-Marín, M. and Uyenoyama, M. K., On the evolutionary costs of self-incompatibility: incomplete reproductive compensation due to pollen limitation. *Evolution*, 2004, **58**, 1924–1935.
70. Ghazoul, J. and Sheil, D., *Tropical Rain Forest Ecology, Diversity, and Conservation*, Oxford University Press, Oxford, New York, 2010.
71. Gigord, L., Lavigue, C. and Shykoff, J. A., Partial self-incompatibility and inbreeding depression in a native tree species of La Reunion (Indian Ocean). *Oecologia*, 1998, **117**, 342–352.
72. Goodwillie, C., Kalisz, S. and Eckert, C., The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. *Annu. Rev. Ecol. Syst.*, 2005, **3**, 47–79.
73. Bawa, K. S., Breeding systems of tree species in a lowland tropical community. *Evolution*, 1974, **28**, 85–92.
74. Friedman, J. and Barrett, S. C. H., Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. *Ann. Bot.*, 2009, **103**, 1515–1527.
75. Friedman, J. and Barrett, S. C. H., The consequences of monoecy and protogyny for mating in wind-pollinated *Carex*. *New Phytol.*, 2009, **181**, 489–497.
76. Charlesworth, D., Why are unisexual flowers associated with wind pollination and unspecialized pollinators? *Am. Nat.*, 1993, **141**, 481–490.
77. Renner, S. and Ricklefs, S. R. E., Dioecy and its correlates in the flowering plants. *Am. J. Bot.*, 1995, **82**, 596–606.
78. Vamosi, J. C., Otto, S. P. and Barrett, S. C. H., Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *J. Evol. Biol.*, 2003, **16**, 1006–1018.
79. Friedman, J. and Barrett, S. C. H., A phylogenetic analysis of the evolution of wind pollination in the angiosperms. *Int. J. Plant Sci.*, 2008, **169**, 49–58.
80. Baker, H. G. and Cox, P. A., Further thoughts on islands and dioecism. *Ann. Mo. Bot. Gard.*, 1984, **71**, 244–253.
81. Stebbins, G. L., Self fertilization and population variability in higher plants. *Am. Nat.*, 1957, **91**, 337–354.

82. Winn, A. A. *et al.*, Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution*, 2011, **65**, 3339–3359.
83. Levin, D. A., The evolutionary significance of pseudo-self-fertility. *Am. Nat.*, 1996, **148**, 321–332.
84. Wendt, T., Canela, B. F., Klei, D. E. and Rios, R. I., Selfing facilitates reproductive isolation among three sympatric species of *Pitcairnia* (Bromeliaceae). *Plant Syst. Evol.*, 2002, **232**, 201–212.
85. Martin, N. H. and Willis, J. H., Ecological divergence associated with mating system causes nearly complete reproductive isolation between sympatric *Mimulus* species. *Evolution*, 2007, **61**, 68–82.
86. Sicard, A. and Lenhard, M., The selfing syndrome: a model for studying the genetic and evolutionary basis of morphological adaptation in plants. *Ann. Bot.*, 2011, **107**, 1433–1443.
87. Glemin, S. and Ronfort, J., Adaptation and maladaptation in selfing and outcrossing species: new mutations versus standing variation. *Evolution*, 2013, **67**, 225–240.
88. Takebayashi, N. and Morrell, P. L., Is self-fertilization an evolutionary dead end? Revisiting an old hypothesis with genetic theories and a microevolutionary approach. *Am. J. Bot.*, 2001, **88**, 1143–1150.
89. Bawa, K. S. and Beach, J. H., Evolution of sexual systems in flowering plants. *Ann. Mo. Bot. Gard.*, 1981, **68**, 254–274.
90. Helbuth, J., Lower species richness in dioecious clades. *Am. Nat.*, 2000, **156**, 221–241.
91. Pellmyr, O., Pollination by animals. In *Plant–Animal Interactions: An Evolutionary Approach* (eds Herrera, C. M. and Pellmyr, O.), Lackwell Publishers, Malden, MA, USA, 2002, pp. 157–184.
92. Bronstein, J. L., Alarcon, R. R. and Geber, M., Tansley review: the evolution of plant–insect mutualisms. *New Phytol.*, 2006, **172**, 412–428.
93. Waser, N. M., Chittka, L. and Price, M. V., Generalization in pollination systems, and why it matters. *Ecology*, 1996, **77**, 1043–1060.
94. Waser, N. M. and Ollerton, J. (eds), *Plant–Pollinator Interactions: From Specialization to Generalization*, University of Chicago Press, Chicago, 2006.
95. Vandermeer, J. K. and Boucher, H., Varieties of mutualistic interactions in population models. *J. Theor. Biol.*, 1978, **74**, 549–558.
96. Briand, F. and Yodiz, P., The phylogenetic distribution of obligate mutualism: evidence of limiting similarity and global instability. *Oikos*, 1982, **39**, 273–274.
97. Rentsch, J. D. and Leebens-Mack, J., *Yucca aloifolia* (Asparagaceae) opts out of an obligate pollination mutualism. *Am. J. Bot.*, 2014, **101**, 2062–2067.
98. Cruaud, A. *et al.*, Fig–fig wasp mutualism: the fall of the strict cospeciation paradigm? In *Evolution of Plant–Pollinator Relationships, Systematic Association Special* (ed. Patiny, S.), vol. 81, 2012, pp. 68–102.
99. Machado, C. A., Robbins, N., Gilbert, M. T. P. and Herre, E. A., Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. *Proc. Natl. Acad. Sci. USA*, 2005, **102**, 6558–6565.
100. Soliva, M. and Widmer, A., Gene flow across species boundaries in sympatric, sexually deceptive *Ophrys* species. *Evolution*, 2003, **57**, 2252–2261.
101. Peter, C. I. and Johnson, S. D., Autonomous self-pollination and pseudo-fruit set in South African species of *Eulophia* (Orchidaceae). *South Afr. J. Bot.*, 2009, **75**, 791–797.
102. Zhou, X., Lin, H., Fan, X. L. and Gao, J. Y., Autonomous self-pollination and insect visitation in a saprophytic orchid, *Epipogium roseum* (D. Don) Lindl. *Aust. J. Bot.*, 2012, **60**, 154–159.
103. Micheneau, C., Johnson, S. D. and Fay, M. F., Orchid pollination: from Darwin to the present day. *Bot. J. Linn. Soc.*, 2009, **161**, 1–19.
104. CaraDonna, P. J. and Ackerman, J. D., Reproductive assurance for a rewardless epiphytic orchid in Puerto Rico: *Pleurothallis ruscifolia* (Orchidaceae, Pleurothallidinae) *Caribb. J. Sci.*, 2012, **46**, 249–257.
105. Biesmeijer, J. C. *et al.*, Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 2006, **313**, 351–354.
106. Potts, S. G. *et al.*, Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.*, 2010, **25**, 345–353.
107. Burkle, L. A., Marlin, J. C. and Knight, T. M., Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, 2013, **339**, 1611–1615.
108. Tylianakis, J. M., The global plight of pollinators. *Science*, 2013, **339**, 1532–1533.
109. Winfree, R., Bartomeus, I. and Carivea, I., Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst.*, 2011, **42**, 1–22.

ACKNOWLEDGEMENT. I thank the Indian National Science Academy (INSA), New Delhi for awarding a position of INSA Honorary Scientist.

Received 22 January 2015; revised accepted 13 July 2015

doi: 10.18520/v109/i7/1255-1263