Colloquium

Reproductive systems and evolution in vascular plants

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Differences in the frequency with which offspring are produced asexually, through self-fertilization and through sexual outcrossing, are a predominant influence on the genetic structure of plant populations. Selfers and asexuals have fewer genotypes within populations than outcrossers with similar allele frequencies, and more genetic diversity in selfers and asexuals is a result of differences among populations than in sexual outcrossers. As a result of reduced levels of diversity, selfers and asexuals may be less able to respond adaptively to changing environments, and because genotypes are not mixed across family lineages, their populations may accumulate deleterious mutations more rapidly. Such differences suggest that selfing and asexual lineages may be evolutionarily short-lived and could explain why they often seem to be of recent origin. Nonetheless, the origin and maintenance of different reproductive modes must be linked to individual-level properties of survival and reproduction. Sexual outcrossers suffer from a cost of outcrossing that arises because they do not contribute to selfed or asexual progeny, whereas selfers and asexuals may contribute to outcrossed progeny. Selfing and asexual reproduction also may allow reproduction when circumstances reduce opportunities for a union of gametes produced by different individuals, a phenomenon known as reproductive assurance. Both the cost of outcrossing and reproductive assurance lead to an over-representation of selfers and asexuals in newly formed progeny, and unless sexual outcrossers are more likely to survive and reproduce, they eventually will be displaced from populations in which a selfing or asexual variant arises.

The world's quarter of a million vascular plant species (1) display an incredible diversity of life histories, growth forms, and physiologies, but the diversity of their reproductive systems is at least as great. In some ferns, individual haploid gametophytes produce both eggs and sperm. In others, individual gametophytes produce only one or the other. In seed plants, pollen- and ovule-producing structures may be borne together within a single flower, borne separately in different structures on the same plant, or borne on entirely different plants. In both groups of plants, the pattern in which reproductive structures are borne influences the frequency with which gametes from unrelated individuals unite in zygotes, and it is a predominant influence on the amount and distribution of genetic diversity found in a species.

Evolutionary explanations for the diversity in mating systems once focused on differences in population-level properties associated with the different reproductive modes. Selfing or asexual plants were, for example, presumed both to be more highly adapted to immediate circumstances and to be less able to adapt to a changing environment than sexual outcrossers, and these differences were used to explain the association of different reproductive modes with particular life histories, habitats, or both (2, 3). We now realize that to explain the origin and the maintenance of particular reproductive modes within species we must relate differences in reproductive mode to differences that are expressed among individuals within populations (4). Nonetheless, differences in rates of speciation and extinction may be related to differences in reproductive modes. As a result, understanding broad-scale phylogenetic trends in the evolution of plant reproductive systems will require us to learn more about the patterns and causes of those relationships.

Modes of Reproduction

In higher animals, meiosis produces eggs and sperm directly. The sexual life cycle of vascular plants is more complex. Multicellular haploid and diploid generations alternate. Diploid sporophytes produce haploid spores through meiosis, and those spores develop into multicellular haploid gametophytes. In pteridophytes (ferns, club mosses, and horestails) the gametophyte is free-living. In seed plants (gymnosperms and angiosperms) the female gametophyte is borne within the ovule and only the male gametophyte (pollen) leaves the structure in which it was produced. Gametophytes produce haploid egg and sperm through mitosis, and these unite to form diploid zygotes from which new sporophytes develop. Asexual reproduction in plants, as in animals, occurs when offspring are produced through modifications of the sexual life cycle that do not include meiosis and syngamy (see Fig. 1).

When vascular plants reproduce asexually, they may do so either by budding, branching, or tillering (vegetative reproduction) or by producing spores or seed genetically identical to the sporophytes that produced them (agamospermy in seed plants, apogamy in pteridophytes). Vegetative reproduction is extremely common in perennial plants, especially in grasses and aquatic plants, and it can have dramatic consequences. The water-weed *Elodea canadensis*, for example, was introduced into Britain in about 1840 and spread throughout Europe by 1880 entirely by vegetative reproduction (6). Exclusive reliance on vegetative reproduction is, however, the exception rather than the rule. More commonly, species like white clover (*Trifolium repens*), reproduce both through vegetative reproduction and through sexually produced seed (7).

Agamospermy is less widespread than vegetative reproduction, although it has been reported from at least 30 families of flowering plants (6, 8), and it is especially common in grasses and roses. Agamospermous species are often polyploids derived from hybridization between reproductively incompatible progenitors. When they have arisen many times, as in the hawk's beards (*Crepis*) of western North America (9) or European blackberries (*Rubus*; ref. 10), the pattern of variation makes it difficult to identify distinct lineages that can be called species. The taxonomic distribution of apogamy in pteridophytes is not well known because of the technical difficulties associated with studying spore development. Nonetheless, Manton (11) cites examples from at least seven genera of ferns and points out that it has been known for more than a century that apogamy can be experimentally induced in many other groups (12).
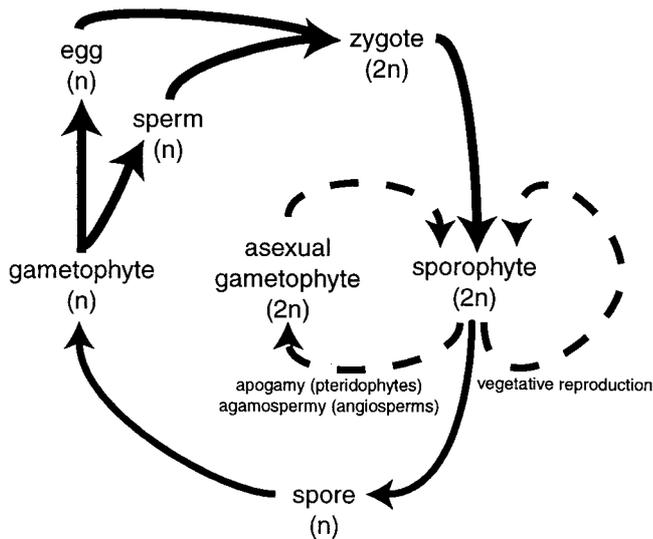
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Fig. 1 Diagram of basic vascular plant life cycles. Asexual life cycles are indicated with dashed lines. The sexual life cycle is indicated with solid lines. See ref. 5 for a more complete description of asexual life cycles.

When vascular plants reproduce sexually, the reproductive structures may be borne in many different ways. In some pteridophytes, like the club moss *Selaginella*, and in all seed plants, eggs and sperm are produced by different gametophytes. In other pteridophytes a single gametophyte may produce both eggs and sperm, as in most ferns. Even when eggs and sperm are produced on the same gametophyte, however, zygotes most frequently are formed through union of eggs and sperm from different gametophytes (13). Differences in the time at which male and female reproductive structures form often are reinforced by antheridiogens released by gametophytes in female phase that induce nearby gametophytes to remain in male phase (14). The antheridiogen system of *Cryptogramma crispa*, for example, appears to enforce outcrossed reproduction even though individual gametophytes are developmentally capable of producing both eggs and sperm (15).

Eggs and sperm are produced by different gametophytes in flowering plants, but anthers and stigmas most often are borne in a single flower. Despite the apparent opportunity for self-fertilization, zygotes most frequently are formed through the union of eggs and sperm derived from different plants (16). Genetically determined self-incompatibility mechanisms appear to have evolved several times in flowering plants (17), but differences in the time at which pollen is released and stigmas are receptive within a flower and spatial separation between anthers and stigmas promote outcrossing, even in many self-compatible plants (18, 19). In some species of flowering plants a polymorphism in stigma height is associated with a complementary polymorphism in anther height, a condition known as heterostyly. Short anthers are found in flowers with long stigmas and vice versa. Darwin (20) described the classic example of this system in *Primula veris*. In that species as in many others, morphological differences are associated with compatibility differences that allow pollen derived from short anthers to germinate only on short stigmas and pollen derived from long anthers to germinate only on long stigmas (see also ref. 21). In other species of flowering plants and in all gymnosperms sexual functions are separate from one another. Either pollen and ovules are produced in different structures on the same plant (monoecy) or they are produced on different plants (dioecy). The separation of sexual functions also may be associated with physiological and ecological differences between the sexes, as in

Siparuna grandiflora in which females and males have different patterns of distribution within populations (22).

Consequences of Reproductive Systems

The genetic structure of a species comprises the identity and frequency of genotypes found within populations and the distribution of genotypes across populations. The reproductive system has long been recognized as a predominant influence on the genetic structure of plant species. Asexual progeny are genetically identical to the individuals that produced them, except for differences caused by somatic mutation. Selfed progeny may differ from their parent as a result of segregation at heterozygous loci, but selfing usually produces far fewer genotypes among offspring than outcrossing. As a result, fewer genotypes usually are found in populations in which either form of uniparental reproduction is common than in those in which outcrossing is the norm.

Among sexually reproducing species, selfers have populations with a smaller and more variable effective sizes (23) and with less exchange of alleles among individuals within and among populations. As a result, selfing species are usually more homozygous than close relatives and have fewer genotypes per population than outcrossers. They also typically have fewer polymorphic loci and fewer alleles per polymorphic locus than closely related outcrossers (24, 25). In addition, the diversity found within selfing species is more a result of differences among populations than of differences among individuals within populations. Over 50% of the allozyme diversity found in selfers is attributable to differences among populations, whereas only 12% is attributable to differences among populations in outcrossers (26).

Allozyme and restriction site analyses of chloroplast DNA (cpDNA) in *Mimulus* (Scrophulariaceae) and nucleotide sequence analyses of introns associated with two nuclear genes in *Leavenworthia* (Brassicaceae) illustrate the dramatic impact mating systems can have on the genetic structure of plant species. In *Mimulus* both allozyme and nucleotide sequence diversity in a selfing species are only one-fourth that of a closely related outcrossing species (27). The lower nucleotide diversity in cpDNA might not be expected, because it is maternally inherited, but in highly selfing species background selection against deleterious alleles at nuclear loci can substantially reduce diversity in both nuclear and cytosolic genomes (28, 29). In *Leavenworthia* populations of selfers are composed almost entirely of a single haplotype at each of the two loci studied, and each population is characterized by a different haplotype. In outcrossers, on the other hand, individuals belonging to the same population are only a little more similar to one another than were individuals belonging to different populations (30, 31). In addition, balancing selection appears to be responsible for maintaining an electrophoretic polymorphism at the locus encoding phosphoglucose isomerase in outcrossing species of *Leavenworthia* (32). Thus, selfers may have lower individual fitness than outcrossers, because they are genetically uniform at this locus.

The consequences of asexual reproduction are in some ways similar to those of selfing. In a strictly asexual population there is no exchange of genes among family lines, just as there is none within a completely selfing population. In contrast to selfers, however, asexual genotypes reproduce themselves exactly, except for differences caused by somatic mutation. Thus, the frequency of heterozygotes can be large in asexual populations even if the number of genotypes found is quite small, especially because many apogamous or agamospermous plants are derived from products of hybridization (8, 11, 33). Agamospermous *Crepis* in western North America, for example, are polyploids derived from hybridization between different pairs of seven narrowly distributed diploid progenitors (9), and local populations are composed of relatively few genotypes. Moreover, most of the genetic diversity in the entire set of agamospermous

species, which are facultatively sexual, is attributable to multiple origins rather than sexual recombination (34, 35).

Although asexual populations are virtually guaranteed to have many fewer genotypes than sexual populations with similar allele frequencies, the number of genotypes within a population can still be quite large. Allozyme studies revealed between 15 and 47 clones in populations of the salt-marsh grass *Spartina patens* on the east coast of North America (36) and 13–15 clones of the daisy *Erigeron annuus* (37). When the number of genotypes per population is large, however, most genotypes are found in only one population and only a few are found in more than two or three populations (38). When the number of genotypes per population is small, as it often is in agricultural weeds, each one may be quite widespread. More than 300 distinct forms of skeleton wire-weed, *Chondrilla juncea*, are found in Eurasia and the Mediterranean, but none is widespread. In Australia, however, only three forms are found, but each is widespread and the species is a serious agricultural pest (39, 40).

In addition to effects on variation at individual loci, both selfing and asexuality may reduce the ability of populations to respond to a changing environment via natural selection, because they reduce the amount of genetic variability in populations. By exposing recessive alleles to selection, selfing may promote the loss of currently deleterious alleles that would be adaptively advantageous in other environments. In fact, selfers may maintain as little as one-fourth of the heritable variation outcrossers would maintain in a population of comparable size (41). In addition, by preventing gene exchange among family lineages, selfing and asexual populations reduce the diversity of genotypes on which natural selection can act. In fact, the proportion of variation caused by differences among individuals within a family is expected to decline almost linearly as a function of the selfing rate in populations. In completely selfing populations, virtually all genetic differences are differences among maternal families. In outcrossing populations, genetic differences within maternal families are expected to be almost as great as those among maternal families (17). In both selfing and asexual species, therefore, the genetic structure of their populations may limit their ability to respond adaptively to natural selection. Because the causes of this constraint are the same for both types of uniparental reproduction, it is convenient to refer to it as the uniparental constraint.

Empirical analyses of phenotypic variation are consistent with the patterns of variation predicted by uniparental constraint in asexual populations (38), but less so in populations of selfers. Comparisons of closely related outcrossers and selfers in *Phlox*, for example, found that outcrossers had more among family variation in 11 of 20 morphological traits than selfers (42), although the analysis did not distinguish between genetic and environmental effects on morphological differences. A similar study in *Collinsia heterophylla* (Scrophulariaceae), however, estimated genetic components of variance and found no relationship between genetically estimated rates of selfing in populations and the partitioning of genetic variance within and among families (43).

In addition to reducing the ability of populations to respond to a changing environment via natural selection, both selfing and asexuality also reduce a population's effective size (44). As a result, deleterious alleles that would have little chance of drifting to fixation in an outcrossing population may be effectively neutral in one that is mostly or completely self-fertilizing. If such an allele is fixed and if it also reduces the reproductive potential of the population, the population will become smaller, making it possible for alleles that are even more deleterious to drift to fixation. This autocatalytic process, the "mutational meltdown," can lead to population extinction and can do so much more easily in completely selfing or asexual populations than in outcrossing ones (45, 46). It appears, however, that a small amount of

outcrossing in primarily selfing species can greatly retard the rate at which the process occurs.

Both the uniparental constraint and mutational meltdown hypotheses make an important prediction: an obligate selfing or obligate asexual lineage will be more short-lived than an otherwise comparable sexual outcrossing lineage. Unfortunately, phylogenetic analyses of the distribution of selfing and asexuality in plants are too few to allow us to assess this prediction directly. It is, however, a botanical commonplace that selfing species are often derivatives of outcrossing progenitors (see the discussion of selfers in *Arenaria* and *Linanthus* below, for example). Because derivatives must be younger than their progenitors, the average age of selfing species is probably less than that of outcrossing species, suggesting that selfers are also more short-lived.

Evolution of Reproductive Systems

Explanations for the diversity of reproductive systems in flowering plants in terms of a tradeoff between short-term adaptive benefit and long-term flexibility were attractive, in part, because they emphasized the synergistic role of reproductive systems in plant evolution. Because of their impact on the amount and distribution of genetic variation within and among populations, reproductive systems can play an important role in determining the pattern and extent of population responses to natural selection on many other traits. As we have just seen, both obligate selfers and obligate asexuals are expected to harbor less genetic variability and to accumulate deleterious mutations more rapidly than sexual outcrossers, which could limit their ability to respond adaptively to environmental change. As a result, we would expect selfing and asexual lineages of plants to be relatively short-lived. Nonetheless, both selfers and asexuals have evolved repeatedly, and it is vital that we understand the circumstances under which they have evolved.

Failure to recognize the frequency with which self-fertilization has evolved, in particular, has led to many taxonomic mistakes. In *Arenaria* (Caryophyllaceae), for example, *A. alabamensis* is a self-pollinating derivative of *A. uniflora*, and populations of *A. alabamensis* in Georgia are independently derived from those in North and South Carolina. Because the floral features that distinguish *A. alabamensis* from *A. uniflora* are convergently derived, both sets of populations are now included within *A. uniflora* (47). *Linanthus* sect. *Leptosiphon* provides an even more striking example (Fig. 2). Self-fertilization evolved independently at least three times in this group of 10 taxa, and one selfing taxon (*Linanthus bicolor*) appears to have three separate origins (48).

Despite the possible impacts that self-fertilization might have on long-term persistence of populations, we have known for more than 35 years that self-fertilization "can evolve only because of a selective advantage before fertilization" (4). Moreover, there are only two types of advantage that self-fertilization can provide. It can increase reproductive success when lack of pollinators or inefficient pollen transfer limits reproductive success (reproductive assurance), or it can increase success as a pollen parent when pollen devoted to selfing is more likely to accomplish fertilization than pollen devoted to outcrossing (automatic selection) (49). Unfortunately, we are not yet able to predict when selfing will provide either reproductive assurance or an automatic selection advantage.

In *Aquilegia formosa* (Ranunculaceae), for example, pollinator exclusion does not affect seed set, suggesting that individuals are able to self-pollinate to ensure seed set. Hand pollinations increase seed set relative to open-pollinated controls, suggesting that pollen transfer limits reproductive success. Nonetheless, open-pollinated, emasculated flowers set as much seed as open-pollinated, unemasculated flowers, demonstrating that self-pollination provides little reproductive assurance in a species
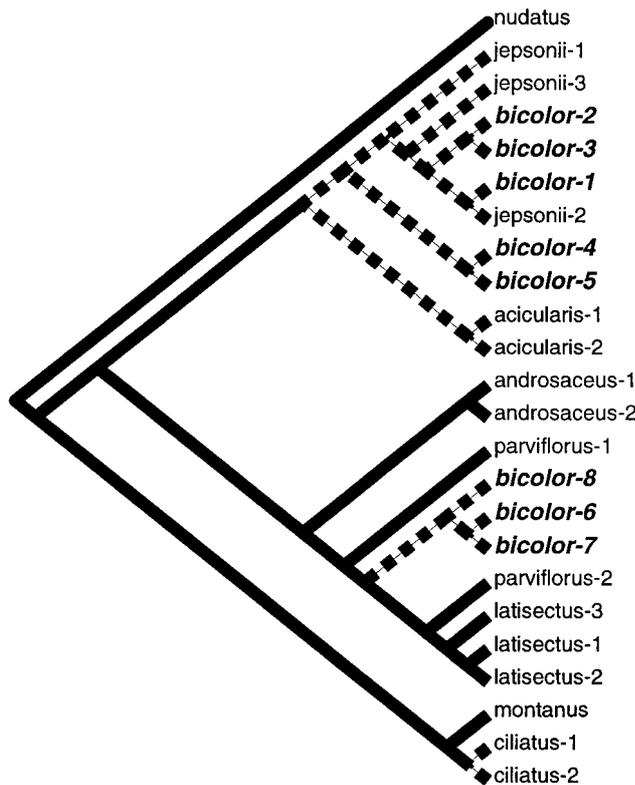
Fig. 2 Phylogeny of *Linanthus* sect. *Leptosiphon* based on 450 bp from the internal transcribed spacer of the nuclear rDNA (redrawn from ref. 48). Hatched branches show lineages where self-fertilization evolved. *Linanthus bicolor* appears in bold, italic print.

where both the capacity for autonomous self-pollination and pollen-limited seed set exist (50).

The automatic selection advantage of self-fertilization, first pointed out by Fisher (51), can arise because in a stable population an outcrossing individual will, on average, serve as ovule parent to one member of the next generation and as pollen parent to one other. A selfing individual in the same population will, however, serve as both ovule and pollen parent to its own selfed progeny and as pollen parent to one outcrossed progeny of another individual in the population. Thus, an allele promoting self-fertilization has a 3:2 transmission advantage relative to one promoting outcrossing. So alleles promoting self-fertilization are expected to spread, unless selfed progeny suffer a compensating disadvantage in survival or reproduction. Fisher's argument assumes that morphological changes promoting self-fertilization do not diminish the selfer's ability to serve as an outcross pollen parent. The extent to which selfing reduces an individual's contribution to the outcross pollen pool is referred to as pollen discounting (52).

Relatively few attempts have been made to measure the extent of pollen discounting in plant populations. In one experiment in *Eichhornia paniculata* (Pontederiaceae) (53) and another in *Ipomoea purpurea* (Convolvulaceae) (54) selfers were actually more successful as outcross pollen parents than outcrossers. In observations derived from natural populations of *Mimulus* (Scrophulariaceae) (55), selfers appeared not to contribute any pollen to the outcross pollen pool. Because the selfers were morphologically quite different from the outcrossers in *Mimulus* and much less so in *E. paniculata* and *I. purpurea*, it may be that differences in the extent of pollen discounting are related to differences in floral morphology. This would be consistent with the observation that pollinator movement within multiple-

flowered influorescences led to observable differences in the degree of pollen discounting in other experiments on *E. paniculata* (56).

Just as the forces favoring evolution of self-fertilization, reproductive assurance, and automatic selection are well-known, so also is the primary force opposing its spread, inbreeding depression. Thomas Knight pointed out more than 200 years ago that the selfed progeny of garden peas are less vigorous and fertile than are outcrossed progeny (57). The impact that inbreeding depression has on the evolution of self-fertilization is, however, more complex than might be expected. The fate of a variant causing an increase in the rate of selfing depends not only on the magnitude of inbreeding depression, but also on the genetic basis of inbreeding depression, and on the magnitude of the difference in selfing rates that the variant induces (see ref. 58 for a detailed review). The complexity arises because different family lineages within a population may exhibit different degrees of inbreeding depression. Because selection among family lines is an important component of natural selection in partially self-fertilizing populations (see above), inbred families (those with a high frequency of alleles promoting self-fertilization) may show less inbreeding depression than less inbred families. If the extent of the association between family inbreeding depression and mating system is strong enough, selfing variants may spread even in the face of high population inbreeding depression (59).

The extent of associations between genetic variants affecting the mating system and levels of inbreeding depression in natural populations is not known. If the genomic rate of mutations to recessive or nearly recessive lethals is sufficiently high, levels of inbreeding depression are relatively insensitive to selfing rates (60), which will cause even families that differ substantially in their selfing rate to have similar levels of inbreeding depression. The relationship between within-population mating system differences and inbreeding depression also may be weak if mating system differences are polygenically controlled (61). Experimental results are mixed. In *Lobelia siphilitica* (Campanulaceae) no differences in inbreeding depression could be found between females, which must outcross, and hermaphrodites, which self to some extent (62), whereas in *Gilia achilleifolia* (Polemoniaceae) individuals with anthers and stigmas well separated (more outcrossing) have greater amounts of inbreeding depression than those in which anthers and stigmas are not well separated (more selfing) (63).

Ideas about the evolution of agamospermy and apogamy in plants tend to focus on the genetic consequences of agamospermy and the mechanisms by which it might arise (5). In flowering plants, for example, agamospermous reproduction resulting from asexual development of gametophytic tissue is almost invariably associated with polyploidy. Whitton (34) suggests that this correlation arises because the same process, formation of unreduced female gametophytes, contributes both to agamospermous reproduction and to the origin of polyploids. Although these arguments may shed light on the evolutionary correlates of agamospermy, they shed no light on the process by which a genetic variant promoting agamospermy is able to establish itself within populations. Fortunately, it is easy to construct arguments parallel to those for the automatic selection advantage of self-fertilization to show why a similar advantage might accrue to asexual plants in a population of hermaphroditic outcrossers.

In a stable population of hermaphrodites, each outcrosser will replace itself, serving once as a seed parent and once as a pollen parent to the outcrossed progeny of another individual. Suppose a genetic variant that causes complete agamospermy is introduced into this population and that this variant has no effect on the pollen production of individuals carrying it. Then an agamospermous individual will replace itself with agamospermous seed, but it also will serve as pollen parent to the outcrossed

progeny of sexual individuals. In short, some of the seed progeny of sexuals will carry the genetic variant causing agamospermy and will be agamospermous themselves, whereas all of the seed progeny of agamosperms also will be agamospermous. Thus, agamospermy has an automatic selection advantage over out-crossing, and it will tend to spread through populations, unless agamosperms have a compensating disadvantage in survival and reproduction relative to outcrossers. I am not aware of studies that investigate the extent of the automatic selection advantage agamosperms might have in natural populations.

The Cost of Sex

Mathematical analyses of models for the evolution and mainte-nance of sexual reproduction suggest that asexuals can be favored either because they avoid the ''cost of males'' or because they avoid the "cost of meiosis" (64, 65). The cost of males arises because the number of females in a population more often limits its rate of population growth than the number of males, a consequence of Bateman's principle (66). As a result, an asexual population composed entirely of females may have a higher intrinsic rate of increase and therefore displace an otherwise equivalent sexual population with separate sexes. In hermaph-rodites, however, the cost of males will exist only when vegetative reproduction allows individuals to produce more offspring per unit of resource than reproduction through seed (67) or when selfers or agamosperms are able to divert resources from pollen to seed production (68).

The automatic selection advantage of selfers and agamo-sperms often is attributed to the cost of meiosis. More careful analysis of the similarities between the evolution of selfing and the evolution of agamospermy suggests that cost of meiosis is not an apt description for the forces governing either process. The phrase cost of meiosis refers to the idea that the genetic coefficient of relatedness between individuals and their out-crossed offspring is smaller than the coefficient of relatedness would be between those same individuals and their selfed or asexual offspring. Notice, however, that in a population of complete selfers an agamosperm would not have an automatic selection advantage over selfers because the pollen it produces would not fertilize any ovules. The asexual progeny of an agamosperm are genetically identical to their parent (barring rare somatic mutation) and the selfed progeny of a selfer are genetically variable to the extent that there is segregation at heterozygous loci. Thus, the asexual progeny of an agamosperm are more closely related to their parent than the sexual progeny of a selfer. Nonetheless, the relative fitness of selfed and agamospermous offspring will determine the outcome of natural selection, not the extent to which selfed or agamospermous progeny resemble their parents.

These observations suggest that cost of outcrossing is a better phrase to describe the automatic selection advantage of selfers and agamosperms relative to sexual outcrossers. The cost of outcrossing arises because selfers and agamosperms can serve as pollen parents of progeny produced by sexual outcrossers, but outcrossers are prevented from serving as pollen parents to the selfed progeny of selfers and the asexual progeny of agamo-sperms. So long as pollen devoted to selfing is more likely to accomplish fertilization than pollen devoted to outcrossing (49) and so long as agamosperms are able to serve as pollen parents to the outcrossed progeny of other individuals, selfing and agamospermy will be over-represented in newly formed progeny of the next generation. Unless, natural selection against selfed or agamouspermous progeny is sufficiently strong, the cost of outcrossing will cause the frequency of outcrossers to decline.

Conclusions

The direct genetic consequences of self-fertilization and asexual reproduction are quite different. Self-fertilization causes prog-eny to be heterozygous at only half as many loci, on average, as their parents, and highly selfing populations are composed primarily of homozyous genotypes. Asexual reproduction, how-ever, results in progeny that are genetically identical to their parents, barring somatic mutation, and asexual populations therefore may be highly heterozygous. Because self-fertilization and asexual reproduction both prevent exchange of genetic material among family lineages, however, the number of geno-types found in populations of predominant selfers or obligate asexuals is usually much smaller than would be found in a population of sexual outcrossers with the same allele frequen-cies. For similar reasons, surveys have repeatedly shown that a greater proportion of the genetic diversity found in selfing or asexual species is a result of differences among populations than in sexual outcrossers (24–26, 69). In short, the great diversity of reproductive systems exhibited by vascular plants is matched by a similar diversity of genetic structures within and among their populations. Indeed, the diversity of reproductive systems may be the predominant cause of the diversity in genetic structure.

Differences in genetic structure associated with differences in reproductive systems were once commonly invoked as evolu-tionary forces governing their origin (3, 70, 71). Although such differences may help us to understand why some lineages persist and diversify and others do not, we now realize that to under-stand the origin of alternative reproductive systems we must look for benefits and costs associated with individual survival and reproduction. Moreover, the comparison of self-fertilization and agamospermy shows that the most important distinction for hermaphroditic organisms is between uniparental and biparen-tal forms of reproduction. Uniparental reproduction, whether through selfing, agamospermy, or apogamy, excludes sexual outcrossers from contributing to some offspring that will form the next generation. If selfers, agamosperms, or apogams are able to contribute to some sexual offspring, genotypes promoting that mode of reproduction will be over-represented in the next generation, reflecting the cost of outcrossing.

To the segregational cost of outcrossing can be added another: selfers, agamosperms, and apogams are able to produce off-spring even under conditions that prevent the union of gametes produced by different individuals. The benefit of this reproduc-tive assurance seems so apparent that it is surprising how few experimental studies have been done to document it and how equivocal their results are (50). When plants reproducing uni-parentally benefit from reproductive assurance or are over-represented in the next generation as a result of donating gametes to the outcrossed progeny of other individuals, they eventually will replace sexual outcrossers in the population, unless the progeny of sexual outcrossers are substantially more likely to survive and reproduce. Thus, the relative fitness of different types of individuals competing in a population and the frequency with which different types are formed will determine whether outcrossers persist in the short term or are replaced by selfers or asexuals.

In the long term, however, differences in the ability of outcrossers, selfers, and asexuals to respond to environmental change and resist the accumulation of deleterious alleles may cause lineages with different reproductive systems to persist for different lengths of time. The smaller number of genotypes in highly selfing and asexual populations may reduce the efficiency with which natural selection can operate, limiting the ability of their populations to respond adaptively to a changing environ-ment—the uniparental constraint. In addition, highly selfing populations have an effective size only about half that of an outcrosser with the same number of individuals (44), and their size also tends to be more variable (23). Both selfers and asexuals, therefore, are more likely to accumulate deleterious mutations than sexual outcrossers, and these mutations could

decrease their reproductive capacity and contribute to their early extinction through a mutational meltdown (45, 46).

In this sense, therefore, Stebbins (3), Grant (70), and Baker (71) were right to contend that selfers and asexuals lack the long-term flexibility characteristic of sexual outcrossers. Indeed, this lack of flexibility may explain why selfers and asexuals originate frequently from outcrossing ancestors, but often seem to be evolutionarily short-lived. If we are to have a comprehensive understanding of broad-scale evolutionary patterns in plants, therefore, we must begin to investigate the relationships among reproductive systems, rates of speciation, and rates of extinction, and we must begin to understand the causes of the relationships we find.

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