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Dioecy and Gametophytic Self-Incompatibility: Reproductive Efficiency Revisited

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NOTES AND COMMENTS

DIOECY AND GAMETOPHYTIC SELF-INCOMPATIBILITY:
REPRODUCTIVE EFFICIENCY REVISITED

By examining the ecological features of different plant mating systems, it may be possible both to identify which selective forces have produced the wide diversity of mating systems in flowering plants and to gain insight as to why one mating system might evolve rather than another (Thomson and Barrett 1981; Givnish 1982; Willson 1982; Baker 1984). For species that are obligately outcrossing, one possible method of comparison involves a quantitative assessment of the efficiency with which plants having different mating systems convert outcross mating opportunities (pollen vector movements between plants) into successful mating events (fruit and seed). Anderson and Stebbins (1984) use such a concept of relative efficiency when comparing the mating systems of dioecy and gametophytic self-incompatibility (GSI). Based on results of a crossing experiment in combination with theoretical observations, Anderson and Stebbins argue that dioecy provides flowering plants with a greater likelihood of mating success. Although accepted by later authors (Bawa et al. 1985; Zavada and Taylor 1986; Cox 1988; Anderson and Symon 1989), their statement contradicts the widely held view that dioecy is a comparatively inefficient breeding system (Mather 1940; Whitehouse 1950; Baker 1959, 1967, 1984; Heslop-Harrison 1972; Richards 1986, p. 290).

The goal of this note is to demonstrate that, contrary to Anderson and Stebbins's (1984) conclusion, GSI is the more efficient outcrossing mechanism. For this discussion, relative efficiency will be treated as the ratio of mating successes to mating opportunities, in which opportunities are represented by the transport of outcrossed pollen by vectors. Defining efficiency in a currency of vector movements provides a measure that can be applied to outcrossing plants with both biotic and abiotic vectors. I first present a quantitative, theoretical framework for interpreting reproductive efficiency for both GSI and dioecy. Next I reexamine Anderson and Stebbins's methods and show why their conclusions are not justified. I then consider the theoretical expectations in the context of three ecological factors important to plant mating systems: pollinator behavior, the spatial structuring of natural populations, and the occurrence of mating among relatives. I end by suggesting that, although mating system efficiency may hold ecological

importance, it is unlikely to have played an important role in the evolution of outcrossing mechanisms for flowering plants.

MATING SUCCESS: A REANALYSIS

The most common form of self-incompatibility for flowering plants is GSI, in which incompatibility is determined by a single, multiallelic locus (Arasu 1968; Richards 1986, p. 198). Because there is no dominance, all individuals in a GSI population are necessarily heterozygous at the self-incompatibility (S) locus. Although the minimum number of alleles necessary for a GSI system to operate is three, estimates of allele number in natural populations range from 28 to several hundred (de Nettancourt 1977; O'Donnell and Lawrence 1984). Only matings between individuals with identical genotypes at the S locus are prevented. A mating between two plants that share one allele in common (i.e., S_1S_2 and S_2S_3 individuals) is possible, although in either direction only half of the pollen (grains with the nonshared alleles) can succeed in fertilizing ovules. Frequency-dependent selection will cause S alleles to increase when rare (Nagylaki 1975). For a GSI system with n alleles ($n \geq 3$), the expected frequency at equilibrium is $1/n$ for each allele (Wright 1939; Nagylaki 1975). All S-locus genotypes will be present at an equilibrium frequency of $2/n(n - 1)$. For three alleles there are three genotypes at equilibrium frequencies of 0.333, while for 30 alleles each of the 435 genotypes is present at a frequency of 0.0023.

If random pollen vector movements occur in a population with GSI that is at equilibrium for S-allele frequencies, the probability that a vector movement between plants results in an incompatible cross is equal to the frequency of each S-locus genotype. When $n = 3$, this probability is maximized at 0.33. For some compatible crosses, one allele will be shared in common between the pollen and ovule plants so that only half of the pollen can succeed (half-compatibility). With only three S alleles, all compatible crosses will involve half-compatibility. With 30 S alleles, however, only 13% of compatible crosses will involve plants that share a common S allele (with n alleles the proportion of half-compatible crosses is $4/[n + 1]$).

Half-compatibility may have no consequence if the pollen vector delivers an excess of pollen grains. Alternatively, the incompatible pollen may cause a greater than proportionate decrease in seed set if incompatible pollen clogs the stigmatic surface or interferes with compatible pollen germination or pollen tube growth (Galen et al. 1989). If half-compatible crosses are discounted proportionately (only half successful), the probability of unsuccessful crosses is $2/n$, which is maximized when $n = 3$ at 0.67 (de Nettancourt 1977, p. 56).

If random pollen vector movements occur in a dioecious population at equilibrium for the sex ratio, the probability that a vector movement will result in a noncompatible cross is 0.50 (male-male and female-female movements). This probability does not include the fact that successful mating events can result only from one direction of vector movement (male to female). Only half of the vector movements between compatible plants will provide successful pollen transfer. In contrast, either direction of vector movement can lead to a successful mating for

TABLE 1
RESULTS OF ANDERSON AND STEBBINS'S (1984) CROSSING EXPERIMENT

Species	Cross Number (Successes/Attempt)	% Successful
<i>Solanum caripense</i> (GSI):		
Sib crosses	11/168	6.5
Between localities	275/1,235	23.3
<i>Solanum appendiculatum</i> (Dioecy)	64/102	63.0

compatible pairings in a GSI population. With the directionality of pollen transfer included, the probability of a noncompatible mating event for a dioecious population increases to 0.75. On theoretical grounds, then, I expect GSI to be a more efficient mating system.

Anderson and Stebbins (1984) reached the opposite conclusion from their experimental data. Hand crosses were performed with greenhouse plants grown from seed using two closely related species of *Solanum* (Solanaceae): *Solanum caripense*, which has a GSI system, and *Solanum appendiculatum*, which is dioecious. *Solanum caripense* matings were classified as either crosses between sibs (seeds collected from a single plant) or crosses between plants from different localities (interaccession). The physical distances separating localities for *S. caripense* were not reported. No information was given for *S. appendiculatum* crosses concerning either the genetic relatedness of the plants used or the physical distance separating the parents from which they were collected in the field. The results from the crossing program (table 1) demonstrate that dioecious mating events succeeded at a significantly higher frequency than either class of GSI mating events.

Two features of Anderson and Stebbins's methods likely biased their results in favor of higher success for the dioecious species. First, the treatments did not control for interparent crossing distance for the two species, as the crosses for *S. caripense* involved two extreme distance classes (table 1). Crossing distance is known to affect the probability of fruit set, with intermediate distances sometimes showing the greatest success (reviewed in Waser and Price 1983, 1989). Second, dioecious crosses were apparently restricted to matings between compatible morphs (pollen transferred from males to females), while the GSI crosses must have been conducted randomly with respect to morph compatibility (since S-locus genotypes cannot be visibly distinguished).

The second and more serious of these biases is easily corrected in their data. To determine the relative success as a function of pollination events, each cross should involve two individuals randomly drawn from the population of GSI or dioecious plants. The direction of pollen transfer can then be assigned randomly. Using this method, only half of the dioecious crosses involve compatible pairings (males with females), and only half of these compatible pairings specify a successful direction of pollen transfer (male to female). The number of successful pollinations should therefore be reduced to 25% of the value reported (table 1). Neither

of these corrections would apply to the crosses with the GSI plants, and it is likely that for *S. caripense* this approach is precisely how pairings and direction of pollen transfer were determined for the experiment.

While the corrected frequency of successful pollinations for the dioecious *S. appendiculatum* (15.7%) is still significantly greater than that for *S. caripense* sib crosses ($G = 5.68, P < .05$), it does not differ significantly from that of the *S. caripense* interaccession crosses ($G = 2.57, P > .10$). The significant difference observed between sib and interaccession GSI crosses for *S. caripense* ($G = 27.97, P < .001$) probably reflects both true incompatibility and inbreeding depression (Charlesworth and Charlesworth 1987). The statement by Anderson and Stebbins that "with dioecy more crosses are legitimate (no S-allele interactions), and consequently fruit set is higher" (p. 425) is incorrect.

NATURAL POPULATIONS

The theoretical conclusions described above are based on the assumption that vectors transport pollen randomly between individual plants. For dioecious species, however, there are two ecological features of natural populations that decrease the likelihood of random pollen vector movement. Both features are expected to further decrease the efficiency of dioecy relative to GSI. First, the sexes in dioecious species sometimes differ in the rewards they offer to animal pollinators (Lloyd and Webb 1977). When rewards are sexually dimorphic, this situation can lessen the likelihood of successful pollen transfer from male to female plants because pollinators may actively discriminate against one of the sexes. Such discrimination has been noted for a number of dioecious species (Kaplan and Mulcahy 1971; Baker 1976; Appanah 1982; Kay 1982; Werf 1983; Kay et al. 1984; Kevan and Lack 1985; Ågren et al. 1986; Muenchow 1986; Bierzychudek 1987; Schlessman et al. 1990; Kevan et al. 1990). The ability of animal pollinators to discriminate against the less rewarding sex is offered as one explanation for the retention of nonfunctional sexual organs in some dioecious species (i.e., "cryptic dioecy"; Mayer and Charlesworth 1991). Interestingly, female *Solanum appendiculatum* possess nonfunctional anthers with sterile pollen that may serve to minimize such discrimination by its pollinators (Anderson 1979; Anderson and Levine 1982). Flowers of GSI species are cosexual and homomorphic (Lewis 1979) and likely to be associated with uniform pollinator rewards with respect to S-locus genotypes, which thereby limits the potential for pollinator discrimination.

A second feature often observed for dioecious populations is the nonrandom spatial distribution of males and females, with the consequence that near neighbors are likely to be the same sex morph (Meagher 1980, 1984; Melampy 1981; Barrett and Thomson 1982). This clustering may reflect niche partitioning between the sex morphs (reviewed in Bierzychudek and Eckhart 1988), but it will also occur as a result of vegetative growth (as noted in Barrett and Thomson 1982; Anderson and Stebbins 1984). Such spatial structuring reduces the likelihood of pollen transfer from male to female morphs (Bawa et al. 1985). Gametophytic self-incompatibility genotypes will be spatially associated only to the extent that

genetic distance co-varies with physical distance over the scale on which pollen is transported. As with dioecious plants, vegetative growth may contribute to spatial structuring for GSI species (Handel 1983). The spatial structure of S alleles in natural populations is unknown, but studies attempting to detect a relationship between genetic and physical distance within plant populations have generally been unsuccessful (Waser 1987; Fenster 1991; Schlichting and Devlin 1992).

POPULATION BOTTLENECKS AND BIPARENTAL INBREEDING

A third ecological factor of considerable importance arises as a result of population bottlenecks, when subsequent mating is likely to occur among related individuals. Anderson and Stebbins (1984) discuss this topic at length and erroneously suggest that dioecy is more efficient in allowing for compatible mating events in populations undergoing such biparental inbreeding. Their argument applies both to bottlenecks resulting from long-distance dispersal events and those occurring in situ. The ability to reproduce through biparental inbreeding will increase the probability of establishment in the case of dispersal and lessen the probability of population extinction following any bottleneck. Anderson and Stebbins's experiment does not bear directly on this issue, as the degree of inbreeding (crossing distance) for their dioecious matings was unspecified. On theoretical grounds, they are wrong in asserting that dioecy permits a higher frequency of biparental inbreeding than does GSI.

Both dioecy and GSI may be equally effective at preventing self-fertilization in these ecological circumstances, with occasional selfing expected only under cases of either sexual lability (Freeman et al. 1980; "leaky dioecism": Baker and Cox 1984) or "leaky" self-incompatibility (de Nettancourt 1977, p. 100; Willson 1982). Dioecy affords no special protection against biparental inbreeding (Fisher 1965, p. 139; Lewis 1979). During a dispersal event involving a single multiseeded fruit, noncompatible matings will occur among the progeny from this fruit at the same frequency (0.75) whether they are full or half sibs.

The role played by GSI in preventing matings among relatives is summarized by Fisher (1965, pp. 139–145). The probability of shared incompatibility among the progeny of a fruit is maximized if the pollen parent (S_1S_2) shared one S allele in common with the ovule parent (S_2S_3). In this case, the full-sib progeny will have only two genotypes (S_1S_2 and S_1S_3), and incompatible matings will occur among them 50% of the time. This worst case scenario still allows more biparental inbreeding (50%) than does dioecy. If the pollen (S_1S_2) and ovule (S_3S_4) parents had no common S alleles, four progeny genotypes are possible, and incompatible matings will occur only 25% of the time. If the fruit was multiply sired (Ellstrand and Marshall 1986), the number of S-locus genotypes among the half-sib progeny increases, which further lessens the likelihood that incompatible matings will occur after the dispersal event.

If half-compatibility is considered to have a proportionate effect on crossing success, the probability of incompatible matings among full sibs rises to 0.75 in the case in which their parents shared one S allele or to 0.50 in the case in which their parents had no common S alleles (Bateman 1952; Lewis 1979). Even with

these more stringent conditions, GSI is no less efficient than dioecy and is likely to permit a higher degree of biparental inbreeding.

Because most dioecious and GSI species have perennial, polycarpic life histories with overlapping generations (Baker 1959; Bawa 1980), inbreeding across generations is also of interest. Noncompatible matings between parents and offspring occur for dioecious species as often as noncompatible matings in the population at large. Ovule parents with GSI are always cross-compatible with all of their progeny; only when parents shared one S allele will the pollen parent be incompatible with its progeny (and then only with half; Fisher 1965, p. 144). Consideration of half-compatibility for matings between parents and offspring decreases the probability of a successful mating, but the probability (0.50 for ovule-parent:offspring; 0.75 for pollen-parent:offspring) is still no worse than that for dioecy (Bateman 1952).

Once colonists become reproductively established after a dispersal event, they face a risk of extinction from stochastic forces that will be particularly important if the population size remains small. A comparable risk will be experienced by any population passing through a bottleneck of similar magnitude in situ. In both situations, the reduced population size will lead to an increased level of inbreeding. The extinction risk for the population will be directly related to the probability of compatible matings given biparental inbreeding. Determination of the extinction risk associated with different mating systems is a topic of considerable importance to plant conservation biology (Huenneke et al. 1986). Although much theoretical attention has been directed to determining the number of S alleles that can be maintained by populations of a specified size (reviewed in Wright 1969, p. 402), the question of extinction risk for populations with either GSI or dioecy has not been treated directly (but see Byers and Meagher 1991 for a stochastic model involving sporophytic self-incompatibility).

Stochastic loss of one sex (for dioecy) or all but two S alleles (for GSI) would doom either population to reproductive failure and extinction. The chance of selecting N individuals that are all the same sex is $0.5^{(N-1)}$ for a dioecious population with a 1:1 sex ratio. The chance that a bottleneck of the same magnitude will leave only two S alleles in a GSI population is less $(2/n[n-1]^{[N-1]})$ for n alleles), since S-locus genotypes exist at equilibrium frequencies less than 0.5.

Neither mating system is particularly well adapted to function under restricted population size or during colonization events. It has long been argued that dispersal is more often associated with self-compatibility and cosexuality (i.e., Baker's law: Baker 1955, 1967; Stebbins 1957). If dioecious species appear to be successful as colonists, it is likely due to the associations of dioecy with the perennial habit, unspecialized pollinators, and fleshy multiseeded fruit that are broadly dispersed rather than a consequence of the mating system itself (Baker 1967; Bawa 1980, 1982; Baker and Cox 1984; Thomson and Brunet 1990).

THE EVOLUTION OF EFFICIENCY

When mating system efficiency is measured by the probability of success for a given pollen vector movement, GSI is a more efficient outcrossing mechanism

than dioecy. This view of efficiency holds ecological interest because the availability of pollen vectors (or receipt of compatible pollen) sometimes limits maternal reproductive success for both dioecious species (Bierzuchudek 1981; Flanagan and Moser 1985; Alexander 1987) and species presumed to have a self-incompatibility system (Weller 1980; Arnold 1982; Snow 1982; Gross and Werner 1983; Koptur 1984; Galen 1985; Sutherland 1987; Zimmerman and Pyke 1988). Additionally, selection for self-fertility owing to pollinator limitation has been implicated in the breakdown of both dioecy (Liston et al. 1990) and self-incompatibility (Lloyd 1965; Barrett 1988; Whisler and Snow 1992).

While efficiency may be an ecologically informative measure when used to compare mating systems, it seems unlikely that efficiency has played an important role in mating system evolution. Explicitly, it might be asked whether selection acts on plant mating systems to maximize their efficiency or, alternatively (as suggested by Richards 1986, p. 194), to minimize the number of cross-incompatible matings. Frequency-dependent selection acting at the level of individual plants will equilibrate both the sex ratio in dioecious organisms (Fisher 1958, p. 158; Lloyd 1974*b*; Charnov 1982) and the frequency of S alleles in GSI plant populations (Nagyaki 1975; but see Lawrence and O'Donnell 1981). The equilibration of sex morph or S-locus genotype frequencies in turn will permit either breeding system to operate more efficiently (in terms of compatible mating events) than it would in a population for which these frequencies are unequal. This increase in efficiency is a simple by-product of frequency-dependent selection acting among individuals, however. It would be incorrect to imply that selection among individual plants has directly acted to increase the efficiency of the mating system.

Selection at a level higher than the individual (clade selection; Williams 1992, p. 23) may account for the evolution of mating system efficiency if clades with more efficient mating systems give rise to more descendent clades or are themselves less likely to become extinct (Whitehouse 1950). Either or both of these two conditions may be true, but it remains to be demonstrated empirically that clade selection has played any role in maximizing plant mating systems' efficiency (Lloyd 1974*a*). Indeed, one of the most efficient mating system in plants (autogamous self-fertilization; Richards 1986, p. 344) has been considered by some to be an evolutionary dead end (Stebbins 1957; Jain 1976). Richards (1986) notes that dioecy "rarely seems to last long enough in evolutionary time, or to be successful enough, to establish a dynasty" (p. 287). The greater frequency by which GSI is observed in the world's flora in comparison to dioecy (Charlesworth 1985) might suggest that if efficiency has indeed played a role in clade selection of plant mating systems, it has favored GSI rather than dioecy.

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