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THE EVOLUTIONARY ENIGMA OF MIXED MATING SYSTEMS IN PLANTS: Occurrence, Theoretical Explanations, and Empirical Evidence

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■ **Abstract** Mixed mating, in which hermaphrodite plant species reproduce by both self- and cross-fertilization, presents a challenging problem for evolutionary biologists. Theory suggests that inbreeding depression, the main selective factor opposing the evolution of selfing, can be purged with self-fertilization, a process that is expected to yield pure strategies of either outcrossing or selfing. Here we present updated evidence suggesting that mixed mating systems are frequent in seed plants. We outline the floral and pollination mechanisms that can lead to intermediate outcrossing, review the theoretical models that address the stability of intermediate outcrossing, and examine relevant empirical evidence. A comparative analysis of estimated inbreeding coefficients and outcrossing rates suggests that mixed mating often evolves despite strong inbreeding depression. The adaptive significance of mixed mating has yet to be fully explained for any species. Recent theoretical and empirical work suggests that future progress will come from a better integration of studies of floral mechanisms, genetics, and ecology, and recognition of how selective pressures vary in space and time.

INTRODUCTION

Evolutionary biologists have long been interested in mixed strategies, in which a species uses more than one tactic, each with distinct fitness consequences (Dawkins 1980, Maynard Smith 1982). For example, organisms exhibit mixed strategies for defense against enemies (Fornoni et al. 2004), timing of reproduction (Satake et al. 2001), dormancy (Spencer et al. 2001), and dispersal of offspring (Venable 1985). The maintenance of alternative tactics within populations is presumed to involve

frequency-dependent selection or condition-dependence where the tactic an individual uses is influenced by its physiological state or environmental circumstance (Maynard Smith 1982). However, the evolutionary processes that maintain mixed strategies have remained controversial (Flaxman 2000, Plaistow et al. 2004).

This review focuses on the evolution of mixed mating strategies in hermaphroditic plants, where reproduction occurs by both self-fertilization (selfing) and mating with other individuals (outcrossing). The evolutionary transition from outcrossing to predominant selfing has occurred in many plant groups, earning it the reputation as a pathway that "has probably been followed by more different lines of evolution in flowering plants than has any other" (Stebbins 1974). The rate of selfing can vary widely among closely related species and even among populations within species, suggesting that it can respond rapidly to natural selection (Jain 1976). Moreover, the evolutionary shift toward self-fertilization is associated with changes in floral biology, life history, and ecology (Barrett et al. 1996, Ornduff 1969), and has manifold consequences for population genetics and evolution (Charlesworth 1992, Grant 1981, Stebbins 1974, Takebayashi & Morrell 2001). Accordingly, questions surrounding the evolution of self-fertilization and the maintenance of mixed mating systems have remained at the forefront of evolutionary biology.

Whether mixed mating systems of plants are evolutionarily stable has been especially controversial. Here we (*a*) provide a historical and theoretical background to this controversy, (*b*) present new comparative data on the occurrence of mixed mating systems, (*c*) outline the functional mechanisms of mixed mating in terms of floral biology and pollination, (*d*) review theoretical explanations for evolutionarily stable mixed mating systems and the progress with empirically testing them, and (*e*) identify worthwhile opportunities for future research.

HISTORICAL AND THEORETICAL BACKGROUND

Inbreeding Depression Versus Automatic Selection

Like many enduring problems in evolutionary biology, interest in the evolution of mating systems is rooted in the work of Darwin and Fisher (reviewed in Holsinger 1996). Darwin's (1876) experimental demonstrations of inbreeding depression led him to question the adaptive value of self-fertilization. In contrast, Fisher (1941) showed that an allele for self-fertilization should spread in an outcrossing population because it increases its own transmission. Outcrossing individuals are mother to their own seed, whereas selfers are both mother and father to their own seed. All else being equal, an allele for selfing will spread if selfed progeny are at least half as fit as outcrossed progeny (see also Lloyd 1979, Nagylaki 1976).

Twenty years ago, Lande & Schemske (1985) showed that inbreeding depression, the main genetic cost of selfing, is not a constant but should evolve jointly with the level of selfing. As a population inbreeds, deleterious recessive or partially recessive alleles that cause inbreeding depression are expressed in homozygous

form and can be purged by selection. This positive feedback facilitates the spread of an allele that increases selfing in a population that is already partially selfing. Consequently, Lande & Schemske (1985) predicted only two stable endpoints of mating system evolution: predominant outcrossing with strong inbreeding depression ($\delta = 1 -$ [fitness of selfed progeny/fitness of outcrossed progeny] > 0.5) and predominant selfing with weak inbreeding depression ($\delta < 0.5$). To test this hypothesis, Schemske & Lande (1985) collected the available estimates of the proportion of seeds produced through outcrossing (t) for plant species. The generally bimodal frequency distribution of those data supported their prediction and led to the suggestion that mixed mating in many species might represent transitional states or incidental by-products of other adaptive mechanisms (Schemske & Lande 1985). Building on the groundbreaking work of Lloyd (1979), Allard (1975), Jain (1976) and others, this provocative combination of theory and comparative data set the stage for a renaissance of work on plant mating system evolution.

The Distribution of Mating Systems Among Seed Plants

The distribution of outcrossing rates in seed plants is central and contentious evidence in the debate on the stability of mixed mating systems (Aide 1986, Barrett & Eckert 1990, Schemske & Lande 1987, Waller 1986, Vogler & Kalisz 2001), with controversy surrounding both the interpretation and adequacy of data. As a starting point for our review, we updated Schemske & Lande's (1985) analysis of 55 species to include estimates now available for 345 species in 78 families (data available from the authors on request). The distributions from the two surveys differ significantly (likelihood ratio $\chi^2 = 21.1$, df $= 4$, $P = 0.0003$; see Figure 1). Compared to the 1985 analysis, the expanded survey shows a much lower representation of predominantly selfing taxa ($t \leq 0.2$, $\chi^2 = 23.7$, df $= 1$, $P < 0.0001$) such that the marked bimodality of the earlier distribution is no longer apparent. The frequency of species exhibiting what has broadly been classified as mixed mating systems ($0.2 < t \leq 0.8$) has increased from 31% in Schemske & Lande's (1985) analysis to 42% in ours, although this difference is not quite significant ($\chi^2 = 2.5$, df $= 1$, $P = 0.11$).

As with all previous comparative analyses of plant mating system variation, our results should be viewed with caution. Although the updated survey is extensive, the 345 species included are far from a random sample of seed plants. For instance, 44% of the species belong to five families: Fabaceae, Pinaceae, Myrtaceae (mostly *Eucalyptus*), Asteraceae, and Poaceae. Thus, our sample may not be representative of the overall distribution of mating systems, and lack of phylogenetic independence may bias inferences regarding associations between mating systems and ecological or life-history traits (but see Barrett et al. 1996). Importantly, there is likely a bias against estimating t for taxa that are expected to be either completely outcrossing (e.g., strongly self-incompatible) or wholly selfing, and lack of polymorphic markers can preclude estimation of t for highly selfing species. It seems unlikely, however, that the addition of these species would yield a markedly

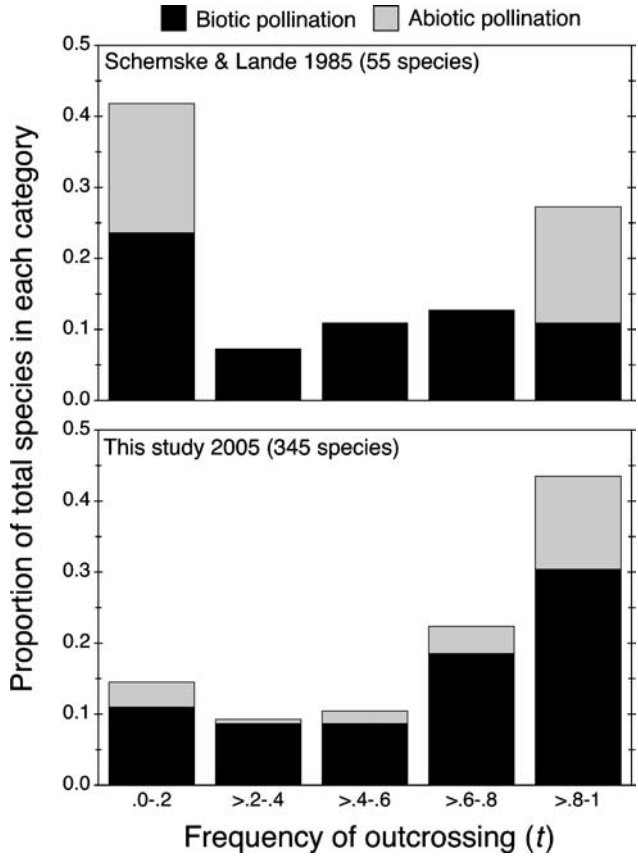

Figure 1 The distribution of estimated outcrossing rates in species of seed plants. The *top panel* shows the distribution of 55 species presented in Schemske & Lande (1985). The *bottom panel* shows the updated distribution of 345 species. The species in each of the five outcrossing categories are classified as biotically pollinated (usually insects, birds or bats) or abiotically pollinated (wind or water). All estimates of *t* are based on at least five maternal plants in natural populations or taken from natural populations and pollinated in a common garden and were derived from the assay of open-pollinated progeny arrays using genetic markers (usually allozyme polymorphisms). When estimates of *t* were available for more than one population of a given species, we averaged across populations. When individual populations were studied for multiple years, we averaged *t* across years before averaging across populations (following Schemske & Lande 1985, Barrett & Eckert 1990).

bimodal distribution, given the relative rarity of strongly selfing taxa (Takebayashi & Morrell 2001). "Apparent selfing" due to biparental inbreeding (sensu Ritland 1984), which is functionally and evolutionarily distinct from true selfing, may produce estimates of $t < 1$ even in fully self-incompatible (SI) or outcrossing species. Finally, estimates of t may differ from the primary, or initial, rate of outcrossing when selection against selfed zygotes occurs between fertilization and sampling of progeny arrays. These issues notwithstanding, our results indicate that mixed mating systems occur frequently in a wide variety of plants, motivating continued exploration of the factors that promote their evolutionary stability.

Emerging Importance of Pollination Ecology

As in previous analyses (Aide 1986, Barrett & Eckert 1990), we find that the distribution of t differs significantly between biotically and abiotically pollinated species (Figure 1; $\chi^2 = 13.1$, df $= 4$, $P = 0.011$), with animal-pollinated taxa almost twice as likely to exhibit a mixed mating system (46.4% of 267 species) than those pollinated by wind or water (26.9% of 78 species, $\chi^2 = 9.8$, df $= 1$, $P = 0.0017$). A higher resolution graphical analysis (Figure 2, following Vogler & Kalisz 2001) indicates that the distribution of t for animal-pollinated species

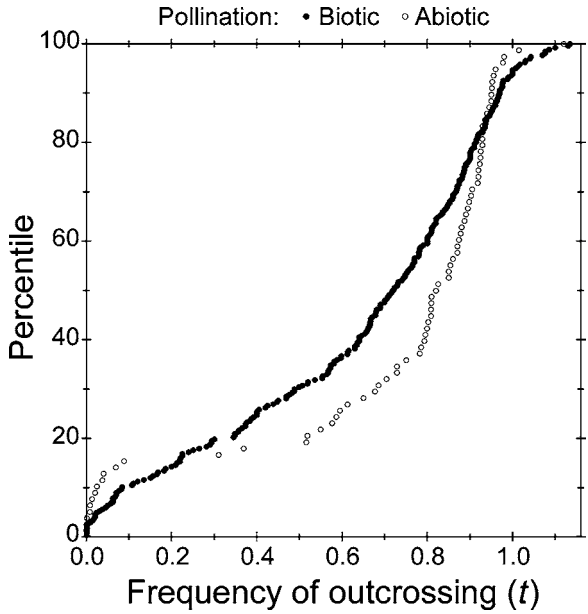

Figure 2 High-resolution distribution of estimated outcrossing (t) for 267 species with biotic pollination (*closed circles*) and 78 species with abiotic pollination (*open circles*). For each pollination mode, species were ranked by estimated t, and ranks were converted to percentiles (y-axis).

is almost continuous, whereas estimates of *t* for abiotically pollinated taxa are concentrated at either endpoint. This may indicate that variability in biotic pollination limits the rate of evolutionary response to selection on the mating system (Schemske & Lande 1986). An alternative explanation is that factors that lend evolutionary stability to mixed mating systems are more prevalent in animal- than in wind-pollinated taxa (Aide 1986, Barrett & Eckert 1990, Barrett et al. 1996, Vogler & Kalisz 2001). Thus, the effects of pollination ecology demand consideration.

Beginning with the landmark work of Lloyd (1979), theoretical studies of the past few decades clarify how selective pressures related to pollination ecology can influence the evolution of mating systems (reviewed in Holsinger 1996). First, selfing can be selected as a mechanism of reproductive assurance, allowing plants to produce offspring when pollinators and/or potential mates are scarce (Lloyd 1979, 1992). Second, selfing can incur the costs of gamete discounting, where self-fertilization reduces production of outcrossed seed (seed discounting, Lloyd 1992), siring of outcrossed seed on other individuals (pollen discounting, Harder & Wilson 1998, Schoen et al. 1996), or both. Third, the ecological costs and benefits of selfing depend on how and when self-fertilization occurs (Lloyd & Schoen 1992). As discussed below, some models incorporating these costs and benefits predict stable mixed mating, addressing the disparity between previous theory and the occurrence of these mating systems in natural populations.

THE MECHANICS OF MIXED MATING

Mixed mating, in which the population outcrossing rate departs significantly from both zero and one, can result from three types of reproductive systems (Cruden & Lyon 1989). First, a genetically based selfing rate polymorphism can exist, as for instance in the relatively rare case where populations contain both self-compatible and self-incompatible individuals (Stone 2002). Second, species can exhibit heteromorphic flower systems (Masuda et al. 2004, Schoen & Lloyd 1984), such as cleistogamous (purely selfing) and chasmogamous flowers (both outcrossing and selfing possible). In the third and by far most common system, individual plants produce a single flower type, and fruits may contain selfed, outcrossed, or a mixture of progeny types (Schoen & Brown 1991). Here, the proportions of selfed versus outcrossed progeny are determined by the timing and relative amount of self- and outcross-pollination and postpollination processes (Holsinger 1991, Kalisz et al. 2004, Lloyd & Schoen 1992).

Modes of Selfing and Their Selective Effects

Self-pollination contributing to mixed mating can occur within (autogamy) or among (geitonogamy) flowers on an individual plant, and within-flower selfing can be either vector-mediated (facilitated) or autonomous. Three modes of autonomous selfing can be distinguished with respect to the period of potential outcross pollen receipt (Lloyd 1979, Lloyd & Schoen 1992). On one end of the continuum is

prior selfing, which occurs before the receipt of outcross pollen. Prior selfing is conferred by early spatial and developmental overlap of male and female functions within a flower (e.g., Fishman & Wyatt 1999), and self-pollination may take place before the flower opens. Competing selfing occurs concurrently with outcross pollen receipt (e.g., Leclerc-Potvin & Ritland 1994), and delayed selfing occurs after the opportunity for outcross pollen receipt has passed. Delayed selfing is achieved through a variety of processes, including developmental changes in stigma-anther position and floral age-dependent breakdown in SI (Lloyd & Schoen 1992, reviewed in Kalisz et al. 1999). With outcross pollen limitation, all modes of autonomous selfing can confer reproductive assurance with little or no pollen and seed discounting (Lloyd 1992, Schoen & Brown 1991). When pollen is not limited, prior and competing selfing can incur costs of gamete discounting, but delayed selfing avoids such costs, because it occurs only after opportunities for pollen export and deposition of outcross pollen. On this basis, delayed selfing is expected to be nearly always advantageous.

In reality, autonomous selfing does not fall into three strict classes nor is floral lifespan invariant. Rather, the timing of autonomous self-pollination is continuously distributed, can be related to floral age or developmental stage (Kalisz & Vogler 2003), and can reflect plasticity in floral longevity (Arathi et al. 2002). A further complication is that the distribution of floral resources may not reflect the timing of pollination. For example, selfed ovules might compete with outcrossed ovules for resources even with delayed selfing.

Facilitated selfing occurs when pollinators transfer pollen from anther to stigma within a flower. This mode of selfing could provide reproductive assurance when mates are scarce, but generally not when pollinators are limiting (but see Anderson et al. 2003). Facilitated selfing is expected to extract high selective costs because of gamete discounting (Lloyd 1992), which has been shown in natural populations (Eckert 2000, Ushimaru & Kikuzawa 1999). Geitonogamy occurs when a biotic or abiotic vector moves self-pollen among flowers on the same plant, the rate of which may be a function of the number of simultaneously open flowers and the pattern of pollinator movement (Eckert 2000, Harder & Barrett 1995, Karron et al. 2004). Like facilitated selfing, geitonogamy offers no reproductive assurance when pollinators are scarce and causes severe or total gamete discounting. Thus, it is considered an unavoidable by-product of selection for outcrossing success if multiple flowers are required to attract a pollinator (reviewed by de Jong et al. 1993, Harder & Barrett 1995) and may impose particularly high costs in pollen discounting because it occurs after pollen has been successfully placed for potential outcross export on the pollinator's body (Lloyd 1992). Although different modes of selfing can be distinguished, some aspects of floral variation are likely to affect more than one mode of selfing (Schoen et al. 1996). For instance, reduced herkogamy (spatial separation of stigma and anthers) or dichogamy (temporal separation of male and female functions) that promotes delayed selfing may also increase the potential for competing or facilitated selfing and enhance the probability of geitonogamy (see Leclerc-Potvin & Ritland 1994). In this case, selection for reproductive assurance

through delayed selfing could result in indirect selection for competing autogamy and geitonogamy (Schoen et al. 1996).

Postpollination Processes

The measured outcrossing rate is frequently higher than that expected from the relative amounts of self versus cross pollen deposited on the stigma (Husband & Schemske 1996). This selective filtering of pollen or zygotes can occur in a variety of forms, including the rejection of self pollen or selfed ovules with SI (de Nettancourt 1997, Dickinson 1994, Lipow & Wyatt 2000, Seavey & Bawa 1986), cryptic SI caused by differential pollen tube growth (Cruzan & Barrett 1993, Eckert & Allen 1997, Jones 1994, Weller & Ornduff 1977), the differential provisioning of outcrossed versus selfed embryos or fruits (Korbecka et al. 2002, Marshall & Ellstrand 1986, Rigney 1995, Stephenson 1981), and the death of selfed embryos expressing lethal recessive alleles (Husband & Schemske 1996, Lande et al. 1994). It is often difficult to identify the actual mechanism of postpollination selection. For example, some forms of late-acting self-incompatibility are difficult to distinguish from early-inbreeding depression (Seavey & Bawa 1986). Many postpollination mechanisms can be environmentally and developmentally plastic (Becerra & Lloyd 1992, Goodwillie et al. 2004, Marshall & Diggle 2001, Marshall & Ellstrand 1986, Vogler et al. 1998). In addition, pre- and postpollination processes can jointly influence the timing of self-fertilization. For instance, in a species of *Agalinus*, self-pollination occurs in the floral bud, but the germination of this self-pollen is delayed (Stewart et al. 1996). In summary, the mechanics of mixed mating are varied and interacting and have complex consequences for selection and the potential for evolution.

THE EVOLUTIONARY STABILITY OF INTERMEDIATE OUTCROSSING: A REVIEW OF THE THEORY AND EMPIRICAL EVIDENCE

The evolution of mixed mating poses a general theoretical problem: What prevents any pure strategy from going to fixation? The stabilizing effects of a wide range of ecological, genetic, and demographic factors have been explored in theoretical models (Table 1). In some, mixed mating is maintained by frequency dependence or some form of negative feedback, whereby increased selfing weakens a factor that selects for selfing. In others, stochastic variation in a selective factor promotes stability of mixed mating through the general principle of nonlinear averaging, or Jensen's inequality. Framed in an evolutionary context, this principle states that the fitness effect in the average environment will differ systematically from the fitness averaged across all environments (Cheptou & Schoen 2002, Morgan & Wilson 2005).

With the striking exception of the "mass action" model of Holsinger (1991), which predicts that selfing can evolve and mixed mating can be maintained

TABLE 1 Selected models that predict stability of mixed mating systems in plants. PD = pollen discounting, RA = reproductive assurance (represented in most cases by seed discounting parameter), δ = inbreeding depression. Models with "fixed" inbreeding depression do not consider its evolutionary dynamics, although expression may be variable. Monomorphic stability describes the evolution and maintenance of a single phenotype with an intermediate rate of outcrossing. With polymorphic stability, variation for outcrossing rate is maintained within populations

Model citation	Phenotypic or genetic	Ecological/ pollination parameters	Inbreeding depression (δ)	Conditions required for stability	Monomorphic/ polymorphic stability
Inbreeding depression					
Holsinger 1986	Genetic	PD, seed dispersal	Fixed, relative fitness of selfed progeny differ depending on dispersal	PD < 1, selfed progeny less successful as migrants, high migration rate	Polymorphic
Holsinger 1988	Genetic	PD	Evolves, mating system and fitness loci not independent	δ overdominant	Monomorphic
Charlesworth & Charlesworth 1990	Genetic		Evolves, mating system and fitness loci not independent	δ overdominant	Both
Uyenoyama & Waller 1991b	Genetic	PD	Evolves, mating system and fitness loci not independent	δ overdominant, low PD	Monomorphic
Latta & Ritland 1993	Genetic	PD	Fixed, modeled in consecutive generations of selfing	Fitness declines with generations of selfing, selfing rate polygenic	Both

(*Continued*)

TABLE 1 (*Continued*)

Model citation	Phenotypic or genetic	Ecological/ pollination parameters	Inbreeding depression (δ)	Conditions required for stability	Monomorphic/ polymorphic stability
Latta & Ritland 1994	Genetic		Evolves, modeled in consecutive generations of selfing	Fitness declines with generations of selfing, δ caused by weakly deleterious alleles	Monomorphic
Rausher & Chang 1999	Genetic		Fixed, differs in male and female function	δ moderate, lower in male than in female expression	Both
Cheptou & Mathias 2001	Phenotypic		Fixed, spatial/temporal variation	δ temporally variable	Both
Cheptou & Schoen 2002	Phenotypic		Fixed, variation among years/generations	δ varies among years/generations	Monomorphic
Cheptou & Dieckmann 2002	Phenotypic	Density regulation, competition	Fixed, expression density-dependent	Wide range, depends on competitive interactions between inbred and outbred progeny	Monomorphic
Biparental inbreeding					
Uyenoyama 1986	Genetic	Biparental inbreeding	Fixed	Biparental inbreeding occurs	Monomorphic
Ronfort & Couvet 1995	Genetic	Population dynamics, limited pollen and seed dispersal	Evolves, purging depends on population structure	Density-dependent recruitment, limited pollen and seed dispersal	Monomorphic

Pollen discounting					
Holsinger 1991	Genetic	PD	None	Whenever selfing can evolve	Polymorphic
Johnston 1998	Phenotypic	PD, RA	Evolves, partial dominance	PD increases with selfing rate, or selfing reduces seed set	Monomorphic
Porcher & Lande 2005c	Both	PD, RA	Evolves, recessive lethals and nearly additive mildly deleterious alleles	Without pollen limitation, substantial PD required. With pollen limitation, $0.9 <$ selfing rate < 1 for all levels of δ and PD	Monomorphic
Pollen limitation/variability					
Schoen & Brown 1991	Phenotypic	RA,variable pollination	Fixed	Pollination environment variable, $\delta < 1$	Monomorphic
Sakai & Ishii 1999	Phenotypic	RA, variable pollination, seed size/number trade-off	Fixed	Optimal seed size small, pollen delivery low and unpredictable	Monomorphic
Vallejo-Marin & Uyenoyama 2004	Genetic	RA, SI	Fixed	Pollen limitation, low *S*-allele diversity	Monomorphic

(*Continued*)

TABLE 1 (*Continued*)

Model citation	Phenotypic or genetic	Ecological/ pollination parameters	Inbreeding depression (δ)	Conditions required for stability	Monomorphic/ polymorphic stability
Morgan & Wilson 2005	Phenotypic	RA, PD, variable pollination, population dynamics	Fixed	Delayed selfing always selected, variable pollination allows intermediate prior selfing	Monomorphic
Resource allocation					
Iwasa 1990	Phenotypic	RA	Fixed	High resource availability, low pollen availability	Monomorphic
Sakai 1995	Phenotypic	RA, PD, pollinator visitation a function of flower size/number	Fixed	Nonlinear constraints on flower size and number with delayed and competing selfing	Monomorphic

regardless of the relative fitness of selfed and outcrossed progeny (see below), most plant mating system theory includes inbreeding depression, which is the key factor that opposes the advantages of selfing. Where the stability of mixed mating is explained theoretically by variation or frequency dependence in other factors, most models find that its maintenance can occur only with certain values of inbreeding depression, although these vary widely among models. In light of Lande & Schemske's (1985) result, the added challenge is to understand the maintenance of some outcrossing given that selective purging of inbreeding depression can generate positive feedback for the evolution of selfing. Most theory on mixed mating assumes a constant value for inbreeding depression (Table 1), and therefore does not account for this potentially destabilizing force. The magnitude of inbreeding depression in species with mixed mating systems and the extent to which purging occurs, then, is relevant to our understanding of mating system dynamics. We turn first to theory and empirical work that explores the evolution of inbreeding depression with the mating system.

The Evolutionary Dynamics of Inbreeding Depression

THEORY In Lande & Schemske's (1985) model, partial selfing was found to reduce equilibrium levels of inbreeding depression, and purging occurred more easily for nearly recessive lethals than for more nearly additive mildly deleterious mutations. The existence of both types of mutation (Charlesworth & Charlesworth 1999, Husband & Schemske 1996) suggests that their combined effect on the dynamics of inbreeding depression are complex. Inbreeding depression may be difficult to purge if the number of lethal recessive alleles maintained with outcrossing is sufficiently high. In this case, very few selfed progeny survive, thus opportunities for purging are diminished (Lande et al. 1994). Other models of partial dominance relax the assumption that the loci influencing inbreeding depression and selfing are independent (Charlesworth et al. 1990, Holsinger 1988, Uyenoyama & Waller 1991a). Holsinger (1988) showed that this allows inbreeding depression to be selectively purged to a greater extent in more selfing lineages. As a result, selfing can evolve at well above the standard threshold of $\delta \leq 0.5$. However, with inbreeding depression caused by partial dominance, interactions between fitness and mating system loci have not been shown to stabilize mixed mating.

In contrast, inbreeding depression caused by overdominance (heterozygote advantage) is expected to increase with selfing under some conditions (Charlesworth & Charlesworth 1987), providing a negative feedback that can maintain mixed mating. This prediction also holds for models that consider the evolution of multilocus genotypes (Charlesworth & Charlesworth 1990, Holsinger 1988, Uyenoyama & Waller 1991b). Several models build on the expectation that inbreeding depression will increase over generations of selfing. Maynard Smith (1977) first suggested that this could stabilize intermediate outcrossing if the selective consequences of selfing differ for inbred and outcrossed plants (see also Damgaard et al. 1992). Using an explicit genetic model, Latta & Ritland (1993) found that this process is

most likely to yield an intermediate *t* when the selfing rate is controlled by many loci. When purging occurs concurrently, intermediate *t* can be stable if inbreeding depression is caused by partially recessive, weakly deleterious alleles (Latta & Ritland 1994). In other words, the short-term negative feedback of consecutive inbreeding on the fitness effects of an allele for increased selfing can more than compensate for the long-term positive feedback of purging, when selection on fitness loci is very mild. Recent theory also suggests that the extent and consequences of purging can be affected by reproductive compensation, a process by which aborted zygotes are replaced by viable ones when resources limit seed production. Reproductive compensation is expected to modify the relations between selfing, inbreeding depression, and genetic load and, under restricted conditions, may stabilize mixed mating (Porcher & Lande 2005b).

EMPIRICAL INVESTIGATION Do the dynamics of inbreeding depression play a central role in either promoting or preventing the stability of intermediate outcrossing? Theory tells us that the answer hinges on its genetic basis. Experiments in which various fitness components are measured through consecutive generations of inbreeding generally detect purging (reviewed in Crnokrak & Barrett 2002), which is inconsistent with the overdominance hypothesis and suggests that partial dominance is the basis of inbreeding depression. Biometric investigations of the genetic basis of inbreeding depression also largely reject overdominance (reviewed in Carr & Dudash 2003, Charlesworth & Charlesworth 1999). Quantitative trait locus (QTL) studies have detected apparently overdominant fitness loci, but these are difficult to distinguish from the effect of deleterious recessive alleles linked in repulsion (reviewed in Carr & Dudash 2003). Experimental evidence for rapid purging is also inconsistent with the hypothesis that intermediate outcrossing is maintained by short-term declines in inbred fitness with recurrent selfing (Damgaard et al. 1992; Latta & Ritland 1993, 1994; Maynard Smith 1977). Declining inbred fitness has been demonstrated in cultivated plant species (Hallauer & Sears 1973), but generally not in natural populations (Dudash 1990, Schoen 1983). In summary, there is relatively little evidence that changes in inbreeding depression associated with the mating system play a positive role in maintaining mixed mating systems.

What is the evidence that purging of inbreeding depression represents a strong destabilizing force? A comparative study of 54 species found significantly lower inbreeding depression in primarily selfing species (mean $\delta = 0.23$) than in primarily outcrossing species (mean $\delta = 0.53$), suggesting that purging is common (Husband & Schemske 1996). In contrast, a meta-analysis of studies comparing inbreeding depression in related species that differ in inbreeding history found only equivocal support for purging (Byers & Waller 1999). The incongruence between the results of these two surveys could reflect differences in timescale; that is, purging might be more consistently detectable in the long term than in the divergence of closely related species or populations. Taken together, experimental and comparative studies indicate that purging occurs but is inconsistent across plant taxa.

Recent theoretical results suggest that a range of factors such as population size and structure can influence purging and standing levels of inbreeding depression (Glemin 2003, Whitlock et al. 2000) and could account for some of this variation.

AN ALTERNATIVE EMPIRICAL ASSESSMENT OF INBREEDING DEPRESSION AND MATING SYSTEMS The strength of inbreeding depression can vary with environmental conditions and is often expressed more strongly under field than greenhouse conditions (Roff 1997). Thus, the evolutionary consequences of inbreeding depression may be hard to predict from studies conducted under benign experimental conditions. An alternative approach is to estimate inbreeding depression from the inbreeding coefficient, F, of mature plants relative to the expected F of progeny based on the selfing rate ($s = 1 - t$; Ritland 1990). In the absence of inbreeding depression, the expected equilibrium value of F for mature plants is $F_e = s/(2 - s)$. Inbreeding depression (δ) reduces F to $F_e = sw/(2 - 2s + sw)$, where w is the fitness of selfed offspring compared to outcrossed offspring (i.e., $w = 1 - \delta$). Inbreeding depression can, therefore, be estimated as:

$$\delta = 1 - 2\left[\frac{(1-s)F}{s(1-F)}\right].$$

This estimator of δ assumes that populations are at inbreeding equilibrium, selfing is the only form of inbreeding, and the marker polymorphisms are neutral and not physically linked to polymorphic loci affecting fitness (Ritland 1990, Charlesworth 1991; for additional discussion of the assumptions of this method see Eckert & Barrett 1994, Routley et al. 1999). It integrates episodes of mortality in natural populations from zygote formation, seed maturation, and dispersal, through survival to reproductive maturity over several years and has generally revealed very strong inbreeding depression (Eckert & Barrett 1994, Herlihy & Eckert 2002, Kohn & Biardi 1995, Routley et al. 1999).

We plotted the estimated F of mature plants against $s = 1 - t$ for 150 species where both parameters were estimated (Figure 3). Overall, mature plants were generally much less inbred than expected in the absence of inbreeding depression. For 88% of the 64 species that exhibited broadly defined mixed mating systems ($0.2 \leq s < 0.8$), F was lower than that expected with no inbreeding depression [i.e., $F < s/(2 - s)$]. Using Ritland's (1990) estimator, mean $\delta \pm$ SD $= 0.81 \pm 0.70$, and inferred $\delta \geq 0.5$ for 72% of species. There are probably large standard errors around any given point (Ritland 1990), and it is possible that the assumptions of this method are violated for some of these species (though most of these violations lead to δ being underestimated). However, it is difficult to envision that some ubiquitous ecological or genetic factor is consistently biasing the estimated F downward and the estimated s upward for such a large fraction of these species. Hence, we view this result as consistent with the possibility that substantial self-fertilization has evolved in many species despite strong inbreeding depression and, conversely, that strong inbreeding depression has been maintained in the face

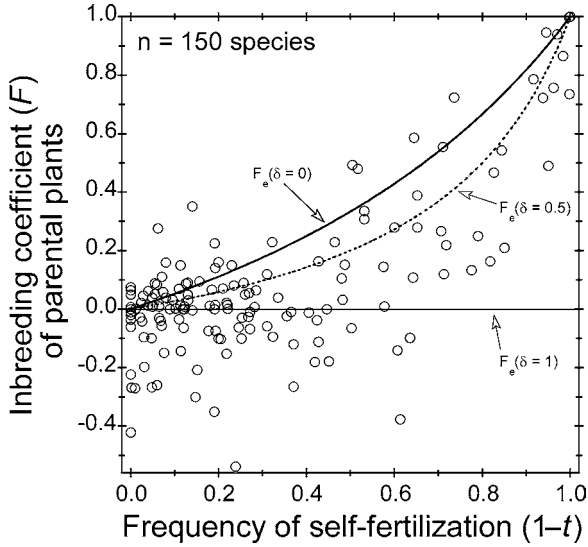

Figure 3 The relation between estimated levels of self-fertilization ($s = 1 - t$) and the inbreeding coefficient (F) of reproductively mature individuals in natural populations of 150 seed plant species. Estimates of t were collected from the literature as described in Figure 1. Estimates of F were from the same populations as t and were usually based on direct assays of mature plants or maternal genotypes inferred from segregation patterns in progeny arrays (usually $\geq$20 maternal genotypes per population). The *heavy solid line* shows the expected relation between s and F in populations at equilibrium (F_e) with no inbreeding depression ($\delta = 1 -$ [fitness of selfed progeny/fitness of outcrossed progeny] $= 0$). The *broken line* shows the equilibrium F if selfed progeny are only half as fit as outcrossed progeny (i.e., $\delta = 0.5$) and the *thin solid line* at $F = 0$ would occur if selfed offspring never survive to reproductive maturity (i.e., $\delta = 1$).

of substantial selfing. What maintains high selfing when selfed offspring are so infrequently recruited into the adult population? This analysis also suggests that some species exhibit substantial outcrossing with weak inbreeding depression. Are those species with low inbreeding depression in transition toward higher selfing rates, or can mixed mating be stabilized by other factors in the face of low δ? We turn our attention to these factors, beginning with theory that explores variation in inbreeding depression.

Variability in Inbreeding Depression

Theory shows that differential expression of inbreeding depression in male and female functions can promote the fixation of an allele conferring intermediate selfing or a stable polymorphism of selfing and outcrossing (Rausher & Chang 1999). In the few taxa for which this has been studied, inbreeding depression is shown to differ in gender expression, but the specific values of inbreeding depression necessary

for stability have generally not been found (Carr & Dudash 1995, Chang & Rausher 1999, del Castillo 1998, Robertson et al. 1994). Although further empirical work is warranted, the limited data available do not suggest a general explanation for mixed mating. Other models indicate that temporal variation in the expression of inbreeding depression can lead to stable mixed mating through the principle of nonlinear averaging (Cheptou & Mathias 2001, Cheptou & Schoen 2002). With temporal variation, the time-averaged fitness of selfed progeny is reduced (Cheptou & Schoen 2002), which provides negative feedback from increased selfing that can stabilize mixed mating. Stochasticity in population density can also lead to stable intermediate outcrossing if competitive interactions cause variation in the expression of inbreeding depression (Cheptou & Dieckmann 2002). Evidence from a few field and greenhouse experiments indicate that competition and stress can influence the expression of inbreeding depression (Cheptou et al. 2000a,b; Eckert & Barrett 1994; Hauser & Loeschcke 1996; Johnston 1992; Wolfe 1993). Nevertheless, the extent of temporal variation of inbreeding depression in the field is largely unexplored. Thus, although these results are theoretically intriguing, their biological relevance has yet to be tested. Finally, a model by Holsinger (1986) explored a form of variation in inbreeding depression in which the relative fitness of selfed and outcrossed progeny differ depending upon whether progeny disperse to a new habitat, which can yield stable intermediate outcrossing. The applications of this model are fairly limited; however it provides one of the first considerations of how a mating system could be affected by ecological and spatial parameters.

Biparental Inbreeding

The potential effects of biparental inbreeding (mating between related individuals) on mating system evolution are complex. Biparental inbreeding reduces the genetic cost of outcrossing because it increases the relatedness of parents to their outcrossed progeny. Its rate is expected to increase with the population selfing rate because, with selfing, individuals in the population come to share more genes that are identical by descent. For this reason, biparental inbreeding might promote frequency-dependent selection that stabilizes intermediate outcrossing (Uyenoyama 1986). Alternatively, biparental inbreeding could have a destabilizing effect in mating system evolution if, as it increases with the selfing rate, it reduces the fitness of outcrossed progeny, thereby reducing realized inbreeding depression (Lloyd 1979, Uyenoyama & Antonovics 1987), a factor not included in Uyenoyama's (1986) original formulation. Mating among relatives can also influence the evolution of inbreeding depression, but the rate of purging depends on parameters of population size and structure (Waller 1993). In a stochastic model, mixed mating was found to be stable when population structure developed through limited pollen and seed dispersal. In this case, biparental inbreeding conferred stability because population structure promoted an increase in inbreeding depression with increased selfing above some threshold selfing rate (Ronfort & Couvet 1995). The ultimate effect of biparental inbreeding on mating system dynamics, therefore, is difficult

to predict and may depend on current levels of inbreeding depression (Uyenoyama & Antonovics 1987, Yahara 1992).

Relatively little empirical work addresses the magnitude and effect of biparental inbreeding on mating system evolution. Pollen and seed dispersal is often limited (Levin & Kerster 1974) but plant populations vary widely in their degree of genetic structure (Heywood 1991, Loveless & Hamrick 1984). Marker-based estimates of selfing rate can include some amount of close biparental inbreeding (Brown 1990, Ennos & Clegg 1982). The amount decreases as the number of marker loci used increases so that biparental inbreeding can be inferred from the difference between the mean single locus and multilocus estimates (Ritland & Jain 1981, Shaw et al. 1981). Inferential estimates of biparental inbreeding vary widely among plant species but tend to be higher in species with mixed mating systems (Brown 1990). Several experimental techniques have been used to distinguish between biparental inbreeding and selfing (Herlihy & Eckert 2004, Kelly & Willis 2002, Lu 2000). For example, Griffin & Eckert (2003) used a transplant experiment to estimate that about 30% of matings involved close relatives in natural populations of *Aquilegia canadensis*. Biparental inbreeding depression, measured either directly through experimental populations (Heywood 1993) or indirectly, by comparing progeny fitness from crosses at different distances (Waser & Price 1994), appears to be substantial in some species. Clearly, the varied effects of population structure on the dynamics of mating systems warrant further attention. Given the wide variation across plant taxa in the extent of biparental inbreeding, comparative approaches might be used to ask whether this factor has a consistent and important effect on mating system dynamics.

Pollen Discounting

Modifications to floral morphology that increase self-pollination can reduce the export of pollen to flowers on other plants (Holsinger 1996). Can pollen discounting provide the negative feedback required to stabilize mixed selfing and outcrossing? In a model that included reproductive assurance, pollen discounting, and purging of inbreeding depression, Johnston (1998) showed that intermediate outcrossing can be evolutionarily stable if pollen discounting increases with the selfing rate as, for example, if evolutionary changes in floral traits that increase selfing incur increasingly higher pollen discounting costs.

Holsinger (1991) found that stable mixed mating could result from frequency-dependent pollination processes. In his mass action model, the selfing rate of an individual is a function of the proportion of self versus outcross pollen grains deposited on its stigma, which in turn is determined by its rate of pollen export and that of other plants in the population. In contrast to genetic models of mating system evolution that balance inbreeding depression against the cost of outcrossing and assume no pollen discounting, Holsinger's (1991) model includes no inbreeding depression and treats pollen discounting as the trait that is selected, yielding an inherent positive relation between pollen discounting and selfing. The model

predicts that, in a highly selfing population, a rare variant that exports pollen will always have a transmission advantage; thus, whenever selfing can evolve, the stable outcome is mixed mating. This process can also maintain mixed mating when inbreeding depression and its evolutionary dynamics are included (Porcher & Lande 2005c). The incorporation of realistic levels of pollen limitation, a factor not considered in Holsinger's (1991) model, yields the expectation of selfing rates that are high but less then one under a wide range of parameters (Porcher & Lande 2005c).

The mass action perspective on mating system evolution yields unexpected and valuable insights, yet the generality of its results may be limited. This approach adds realism to plant mating system theory in that it models the frequency dependence of the selfing rate. However, it may be difficult to reconcile with the floral biology of mating system transitions, in that, for instance, variation in stigma-anther separation could have dramatic effects on the selfing rate with little effect on pollen export. In other words, because it focuses explicitly on pollen discounting, it tells us little about the cases where this parameter is negligible. Moreover, the models assume that self and outcross pollen arrives simultaneously on stigmas. Although strict prior selfing, such as bud pollination, is probably rare, a continuum from prior to competing selfing undoubtedly exists, and autonomous self-pollination may often occur before outcrossing.

Harder & Wilson (1998) extended the mass action approach to a broader array of floral scenarios by considering a more complex partitioning of pollen fates, including a distinction between discounting and nondiscounting sources of self-pollination. Nondiscounting pollen is unavailable for export from the flower, and thus its participation in self-fertilization does not decrease outcross siring. This approach explores how changes in pollen fate affect complex stepwise selection on floral traits that may occur during the evolution of mating systems. It examines the conditions that allow evolutionary shifts between different modes of selfing, a largely unexplored area of theory that is likely to provide insights into the stability of mixed mating. A similar consideration of stepwise changes in ovule fate with floral evolution may also be fruitful.

Despite the potential evolutionary importance of pollen discounting, this parameter is quantified only rarely. The male outcrossing success of plants that vary in selfing rate can be compared using genetic markers and experimental arrays (Chang & Rausher 1998, Fishman 2000, Kohn & Barrett 1994, Rausher et al. 1993). Such studies yield variable estimates and suggest that pollen discounting may sometimes depend on the frequency of selfing variants. For example, Chang & Rausher (1998) show that negative frequency dependence of outcross success can contribute to the mixed mating system of *Ipomoea purpurea*. In a different approach, pollen discounting was estimated in *Erythronium grandiflorum* using a pollen color polymorphism (Holsinger & Thomson 1994). Although measurement of pollen discounting poses formidable challenges, accumulating theoretical results suggest that knowledge of this parameter may be critical to our understanding of mixed mating.

Reproductive Assurance

The often cited "best of both worlds" hypothesis (Becerra & Lloyd 1992, Cruden & Lyon 1989) holds that certain forms of mixed mating evolve because they promote outcrossing but provide reproductive assurance when pollinators or mates are scarce, combining the advantages of both reproductive strategies. This view is supported by the higher frequency of mixed mating systems among taxa pollinated by animals, which may exhibit marked spatiotemporal variation in pollinator service (Eckert 2002, Wolfe & Barrett 1988). Despite its intuitive appeal and frequent invocation, this hypothesis and the role of reproductive assurance have only recently received extensive theoretical attention. Indeed, many mating system models do not include a parameter that allows selfing to increase total seed set, a measure of reproductive assurance (Table 1). Lloyd (1979, 1992) showed that delayed selfing provides reproductive assurance, has no gamete discounting costs, and is therefore nearly always favored, yielding a mixed mating system when outcross pollen is limited. However, the selective value of other forms of selfing can be eroded by seed discounting (Lloyd 1992). Moreover, reproductive assurance selfing in perennials could reduce future survival and discount later production of outcrossed seeds within or between reproductive seasons (Morgan et al. 1997). Thus, selection for reproductive assurance is more complex than might be expected.

Because cross-incompatibility among plants with the same SI genotype can limit mate availability and intensify pollen limitation (Byers & Meagher 1992), reproductive assurance is expected to play a part in the evolutionary breakdown of SI (Charlesworth & Charlesworth 1979, Porcher & Lande 2005a). Theory suggests that, with pollen limitation, partial SI (yielding mixed mating) can be maintained because of the complex interaction of direct selective effects (inbreeding depression, cost of outcrossing, reproductive assurance) and genetic associations between the self-incompatibility (*S*) locus and alleles modifying the strength of SI (Vallejo-Marin & Uyenoyama 2004). The conditions for stability are restrictive in this model, however, requiring a narrow range of inbreeding depression and low *S*-allele numbers, which suggests either that many partially SI species are in transition toward self-compatibility or that other factors can also promote stability.

The models described above consider the evolution of selfing, and mixed mating a consequence when outcross pollen is chronically limited. However, both pollen limitation and selection for reproductive assurance are likely to be variable, which can, in principle, lead to the evolution of stable mixed mating. A simple model that includes variation in pollinator service (Schoen & Brown 1991) gives the result that selfing induced only in the absence of cross-fertilization is selected whenever pollination is variable and $\delta < 1$. In two other models, stability of mixed mating derives from variable pollination and the principle of nonlinear averaging. Morgan & Wilson (2005) use a population dynamic approach and find that the effect of variance in pollen delivery depends on the mode of autonomous selfing. Delayed selfing goes to fixation regardless of variance in pollination, such

that the population outcrossing rate is determined proximately by the level of outcross pollination. In contrast, selection on prior selfing is influenced by the degree of variance in pollination; stable mixed mating is expected for a wide range of parameters. Sakai & Ishii (1999) showed that variable pollination may or may not select for a mixed strategy when the trade-off between seed size and number is considered. In other words, when selfed progeny have lower fitness, it may be better to forego reproductive assurance selfing and make fewer, larger outcross seeds. Accordingly, mixed mating is more likely to be stable when the optimal seed size is small. Thus, the model provides a scenario in which a best of both worlds mating system may not, in fact, be best.

The selective value of reproductive assurance may also change during the course of mating system evolution because autonomous selfing allows populations to grow under conditions where insufficient outcross pollination would otherwise limit reproduction. Cheptou (2004) showed that this, in turn, alleviates outcross pollen limitation, thereby reducing the selective advantage of selfing. Moreover, increased population density may also intensify the expression of inbreeding depression, which could lead to reduced population density. These demographic feedback loops have a variety of counterintuitive consequences, but, interestingly, do not appear to explain stable mixed mating.

A clear theoretical understanding of the role of reproductive assurance in the evolution of mixed mating has not yet emerged, and empirical work lags behind theory. Indirect evidence for reproductive assurance includes autonomous (especially delayed) selfing (e.g., Cheptou et al. 2002, Dole 1992, Rathcke & Real 1993; see also Lloyd & Schoen 1992), reduced pollen limitation in selfing relative to outcrossing populations or species (Goodwillie 2001, Kasagi & Kudo 2003, Larson & Barrett 2000) and low rates of cross-pollination (Burd 1994, Fausto et al. 2001, Ramsey & Vaughton 1996). However, direct tests of reproductive assurance that compare seed set by emasculated flowers versus intact control flowers subjected to open pollination (Schoen & Lloyd 1992) have been carried out for relatively few species with variable results (reviewed in Cruden & Lyon 1989, Elle & Carney 2003, Herlihy & Eckert 2004, Holsinger 1996, Schoen et al. 1996). Moreover, demonstrating that selfing confers reproductive assurance in the face of variable pollination requires substantial temporal and spatial replication of the emasculation experiment (Eckert & Schaefer 1998), which has been attempted only rarely. Kalisz et al. (2004) showed that autonomous delayed selfing increases seed production during years of pollinator failure in three populations of *Collinsia verna*, yielding intermediate outcrossing and reproductive assurance when outcross-pollination is limiting. In contrast, Herlihy & Eckert (2002) found that autonomous selfing always increased seed production in 12 populations of *Aquilegia canadensis*; however the extent of selfing at the population level was unrelated to the degree of pollinator failure. To date, there has been no theoretical investigation of the longer-term, between-season trade-offs of reproductive assurance and seed discounting (Morgan et al. 1997) or empirical studies of how reproductive assurance varies with population demography.

Resource Allocation Models

Reduced allocation to attractive structures (e.g., reduced corolla size) has long been observed in highly selfing plant taxa (Ornduff 1969). Although changes in allocation are often considered to occur in response to evolution of the mating system, they can also be a direct determinant of outcrossing rates, as they affect deposition of outcross pollen and pollen export. The evolution of selfing rate has been modeled as a function of resource allocation to floral structures. In a model of delayed selfing, Iwasa (1990) showed that trade-offs between allocation to pollen capture promoting outcrossing (large flowers) and progeny fitness (inbreeding depression) can result in evolutionarily stable intermediate selfing rates. Sakai (1995) found that when the relationship between flower size and number is considered, mixed mating with delayed or competing selfing can be stable only when that function is nonlinear and flower number is strongly constrained. Empirical testing of the effects of shifts in resource allocation on the evolution of the mating systems has lagged far behind theory, probably because changes in allocation are often interpreted as a secondary adaptation to optimize fitness in response to changes in the selfing rate (reviewed in Ornduff 1969, Takebayashi & Morrell 2001). However, a recent QTL study of the genetics of floral differences between a selfing and a predominantly outcrossing species of *Mimulus* (Fishman et al. 2002) found evidence of linkage and/or pleiotropy between some of the QTLs for traits that directly affect selfing (i.e., herkogamy) and traits involving allocation to attraction (i.e., corolla size). Although it is impossible to determine the order in which various gene (or QTL) substitutions occurred in the transition from selfing to outcrossing, this approach may be valuable for evaluating models of mating system evolution (see discussion in Fishman et al. 2002).

MIXED MATING SYSTEMS: A BROADER PERSPECTIVE

As reviewed here, the challenge to explain the occurrence of mixed mating has inspired remarkably diverse theoretical approaches and hypotheses. Most are directly applicable to only a subset of the mechanisms or modes of selfing that produce mixed mating (Table 1). For example, models of reproductive assurance are most relevant for autonomously selfing species. General models have limited application to partial SI because its stability may be affected by the diversity (Vallejo-Marin & Uyenoyama 2004) and dynamics of *S*-alleles. Few models address the evolution of geitonogamy. Finally, theory that predicts a balanced polymorphism may not be applicable to the evolution of a monomorphic basis for mixed mating. To assess the potential importance of different hypotheses, then, we would like to know the broad distribution of selfing modes and floral mechanisms that produce intermediate outcrossing rates.

To that end, we compiled both anecdotal and experimental information on autonomous selfing, geitonogamy, and postpollination phenomena for the angiosperm species included in our survey (Figure 4, see legend for methods). The

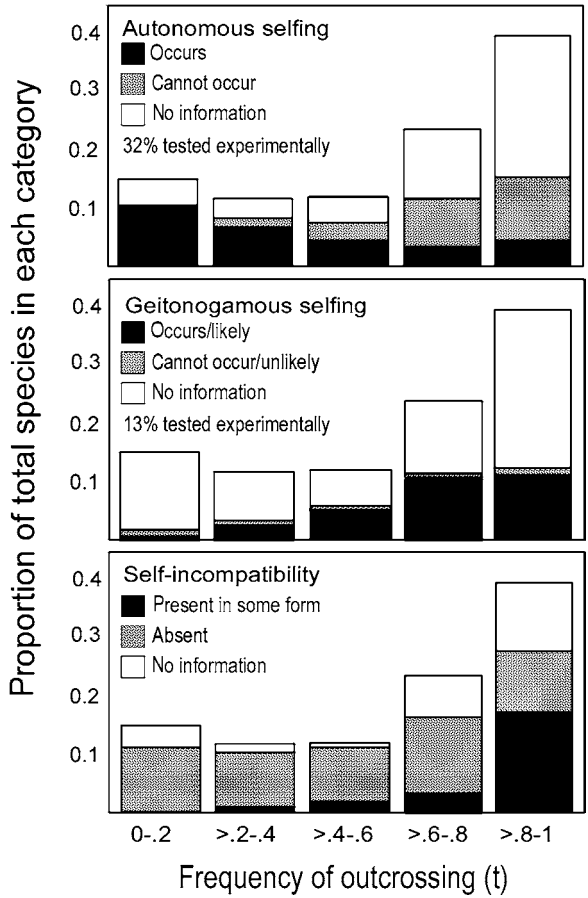

Figure 4 Mechanisms that contribute to the distribution of outcrossing rates in angiosperm species in our survey. Mechanisms that were reported to be only partially effective (e.g., partial SI, partial seed set due to autonomous selfing) were recorded as positive responses. We recorded information from the *t* estimate studies and then searched more broadly for journal articles with additional information on each species. We distinguished between anecdotal evidence (e.g., a verbal hypothesis that geitonogamy is likely or unlikely based upon inflorescence size and pollinator behavior) and experimental results (e.g., bagging experiments to test for autonomous selfing ability) and present the proportion of all species in the data set for which experimental data are available. Data available from the authors on request.

available data are remarkably limited, but support a few preliminary observations. A substantial proportion of the species with intermediate outcrossing ($0.2 < t < 0.8$) are at least partially capable of autonomous selfing, indicating a possible role for reproductive assurance in their mixed mating systems. Although experimental investigations are few, the potential for geitonogamous selfing is relatively common in species with high intermediate outcrossing rates, suggesting that a proportion of selfed progeny in these species may be an indirect result of selection for outcrossing success (e.g., Eckert 2000). SI is relatively common for highly outcrossing species, whereas the majority of species with lower t are reportedly fully self-compatible. Although partial SI may be undetected or attributed to inbreeding depression in some cases, the information available suggests that it is not a primary contributor to mixed mating in the species sampled.

Most strikingly, the proximate mechanisms contributing to the estimated outcrossing rates are unknown for most species. Moreover, for only a small fraction of species surveyed do we have any quantitative information on the mode of self-fertilization (Figure 4). Although detailed studies of reproductive biology have been undertaken for many plant species, these are often not linked to outcrossing rate estimates, limiting their contribution to our understanding of mating system evolution. Progress will come from the compilation of outcrossing estimates with at least basic functional information on floral biology across a broader range of plant species. Moreover, we argue that these mechanisms, when known, must be taken into greater consideration in the valid application of mating system theory.

A more complete understanding of the evolution of mating systems in any species requires that we dissect the rate of selfing into its components parts, identify the floral traits influencing each component, and then experimentally alter these traits in some realistic way to determine the consequences for fitness and hence the evolutionary stability of the resident mating system (Herlihy & Eckert 2004). However, to date, the adaptive significance and evolutionary stability of mixed mating has yet to be fully verified, even for the few species in which the functional aspects and many of the relevant costs benefits have been studied (Barrett 2003).

The literature on plant mating system evolution focuses primarily on what maintains mixed mating systems, rather than assessing whether, or which, existing mixed mating systems are evolutionarily stable. The substantial frequency of species with intermediate t offers evidence that mixed mating systems can be stable, but we have no quantitative expectation as to how frequent mixed mating should be under either hypothesis. A danger inherent in this debate is the creation of a false dichotomy—that mixed mating as a whole is either fundamentally stable or unstable. Phylogenetic studies show that transitions between predominantly selfing and outcrossing states are common in some plant taxa (Goodwillie 1999, Kohn et al. 1996, Wyatt 1988), and we can reasonably assume that some of the existing mixed mating systems are transitional. A more rigorous examination of the frequency of mixed mating systems within a phylogenetic perspective is warranted. The serious biases inherent in surveys of published outcrossing rates could be remedied by systematic efforts, in which species are sampled randomly and intensively from

individual plant families or lineages. Although phylogenetic approaches have been used in the study of breeding system stability (Dorken et al. 2002, Husband & Barrett 1993, Weller et al. 1995), they have contributed surprisingly little to the problem of mixed mating. Most of the phylogenetically based studies of mating or breeding systems use qualitative character states (Barrett et al. 1996, Bena et al. 1998, Goodwillie 1999, Igic et al. 2004, Kohn et al. 1996, Wyatt 1988) and have not considered intermediate outcrossing. Transitional mixed mating should occur only on the tips of branches, whereas the occurrence of deeper phylogenetic lineages with intermediate t would indicate stability. Combining phylogenetic approaches with estimates of inbreeding depression can allow us to ask whether purging is a key determinant in the stability of mixed mating. For example, in *Leptosiphon* (Polemoniaceae), transitions from SI to predominant selfing have occurred multiple times (Goodwillie 1999), and partial SI with mixed mating has been observed in only one species of the genus, *L. jepsonii* (Goodwillie et al. 2004). The phylogenetic data and the finding of low δ in some populations of *L. jepsonii* (Goodwillie 2000) suggest that, in this case, partial SI may represent a transitional state in the breakdown of SI. With the increasing availability of genetic data for both mating system and phylogenetic analyses, such approaches could yield insights in other taxa.

Lande & Schemske's (1985) provocative model has inspired a wealth of studies of inbreeding depression and set in motion the developing theory of mixed mating systems. Although large empirical gaps remain, a broad understanding of the genetic basis of inbreeding depression has emerged (Charlesworth & Charlesworth 1999). In contrast, empirical estimates of the pollination parameters required to test ecological mating system models are still extremely limited. Further theoretical exploration is needed as well. To date no compelling evidence suggests that we have identified factors or processes that can account for mixed mating across a broad range of plant taxa. The conditions for stable mixed mating are restrictive in many models and others have failed to find empirical support. Moreover, existing models do not yet provide an explanation for observed differences in the frequency of mixed mating with biotic versus abiotic pollination. In addition to the recent expansion of theory that emphasizes pollination biology (e.g., Harder & Wilson 1998, Morgan & Wilson 2005, Porcher & Lande 2005c), several promising, largely untested, theoretical directions are emerging that may provide further insights on mixed mating. A common feature is that the evolution of the mating system is considered in a broader context of, for instance, life-history strategies (Morgan et al. 1997, Tsitrone et al. 2003), population dynamics (Cheptou 2004), metapopulation dynamics (Pannell & Barrett 1998, 2001), plant and insect communities (Fausto et al. 2001, Moeller 2005), and coevolutionary interactions between plants and their parasites (Agrawal & Lively 2001, Busch et al. 2004). Indeed, although the search for general explanations for mixed mating is compelling, distinct factors may well be important for its maintenance in different plant taxa. Whether or not unifying explanations are found, the enduring enigma of mixed mating promises to motivate yet more fruitful exploration into the evolution of plant mating systems.

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