

# The Maintenance of Outcrossing in Predominantly Selfing Species: Ideas and Evidence from Cleistogamous Species

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## Key Words

autogamy, inbreeding depression, mixed mating, reproductive strategy, self-fertilization

## Abstract

Cleistogamous species present strong evidence for the stability of mixed mating, but are generally not considered in this context. Individuals of cleistogamous species produce both obligately selfing cleistogamous flowers (CL) and potentially outcrossed chasmogamous flowers (CH) with distinct morphologies. Greater energetic economy and reliability of CL relative to CH suggest that forces that maintain selection for outcrossing may be stronger in these species than in mixed maters with monomorphic flowers. We reviewed data from 60 studies of cleistogamous species to evaluate proposed explanations for the evolutionary stability of mixed cleistogamous and chasmogamous reproduction and to quantify the magnitude of selection necessary to account for the maintenance of CH. We found circumstantial support for existing hypotheses for the stability of cleistogamy, and that forces that maintain CH must account for a 15–342% advantage of reproduction via CL. We suggest that heterosis and the effects of mass action pollination should be considered.

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**Mixed mating:** A combination of selfing and outcrossing within an individual

**Cleistogamous species:** Species in which individuals are capable of producing both chasmogamous and cleistogamous flowers

**Cleistogamous flowers (CL):** Small inconspicuous permanently closed flowers that self-fertilize in the bud

**Chasmogamous flowers (CH):** Open flowers that are potentially outcrossed

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## INTRODUCTION

The pattern of mating among individuals of sexually reproducing species has substantial influence on the process of evolution. The average degree of relatedness among mates determines how genetic variation is distributed among lineages and therefore influences the potential of a species to respond to natural selection. Much of the theory and empirical work concerning the evolution of mating systems has focused on hermaphroditic plants because they exhibit a wide range of variation and a high degree of evolutionary lability in their mating systems. A recent review of this body of work (Goodwillie et al. 2005) highlights the persistent puzzle of what evolutionary forces maintain stable mixtures of self-fertilization and outcrossing. The most general models of mating system evolution conclude that only complete selfing and complete outcrossing are evolutionarily stable, but Goodwillie et al. (2005) report that 42% of 345 species for which data on mating systems is currently available exhibit mixed mating, defined as rates of selfing between 0.2 and 0.8. Although the estimated frequency of mixed mating may be biased by unequal sampling of taxa (e.g., undersampling of obligately outcrossing taxa; Igic & Kohn 2006), it is clear that a substantial number of species do engage in mixed mating.

The appreciable frequency of mixed mating species has stimulated the development of models that incorporate additional forces that could influence mating system evolution. In particular, models have added ecological forces related to pollen transfer with the result that many have identified conditions that allow for stable mixed mating. Goodwillie et al. (2005) compile a list of more than twenty models that have been proposed to explain the adaptive significance and stability of mixed mating, and note that a lack of empirical data rather than theoretical explanations limits our current understanding of mating system evolution.

Cleistogamous species, in which individuals produce a mixture of cleistogamous flowers (CL) and chasmogamous flowers (CH), present a particularly striking challenge to the prediction that mixed mating is not evolutionarily stable. Cleistogamous species may also offer particular insight into selective forces that maintain outcrossing once selfing evolves. CL are highly reduced structures that obligately self-fertilize in the bud. Because CL never reach anthesis, they can neither donate nor receive outcrossed pollen. Most species that produce CL also produce open CH that can participate in outcrossing. The production of both CH and CL by individuals inherently facilitates a mixture of selfing and outcrossing (Darwin 1896). The production of CL appears to have evolved independently in as many as 50 plant families (Culley & Klooster 2007, Lord 1981, Plitmann 1995, Uphof 1938), and there are few reported evolutionary losses of cleistogamy (Campbell et al. 1983, Culley & Klooster 2007, Lord 1981), suggesting that the conditions that favor the evolution and maintenance of cleistogamy are common. Understanding the conditions that favor the stable production of both CH and CL could provide insight into the conditions that favor stable mixed mating in general. Although cleistogamy is well known among botanists, it has rarely been exploited as a tool for testing mating system theory because it entails unusual features that are not accounted for in general models.

The most general models of mating system evolution emphasize the balance between two genetic forces. The major force favoring the evolution of self-fertilization is the automatic fitness advantage to mixed selfing and outcrossing relative to outcrossing alone (Fisher 1941, Jain 1976). This advantage arises because an individual that both selfs and outcrosses gains fitness through siring its own ovules and those of other individuals, whereas a pure outcrosser can only sire ovules produced by other individuals, resulting in a 50% fitness advantage, on average, to mixed selfing and outcrossing. The primary force believed to counter the automatic fitness advantage is inbreeding depression, the reduction in fitness of selfed relative to outcrossed progeny (Charlesworth & Charlesworth 1987, Lande & Schemske 1985, Lloyd 1979). Assuming that outcrossed mates are unrelated, if inbreeding depression is greater than 50%, complete outcrossing is predicted to evolve, and if inbreeding depression is less than 50%, complete selfing should evolve. The automatic fitness advantage is reduced when selfing reduces the amount of pollen a selfer contributes to outcrossing (Feldman & Christiansen 1984, Holsinger et al. 1984, Nagylaki 1976), an effect described as pollen discounting. Pollen discounting lowers the threshold inbreeding depression required for complete outcrossing to evolve (Holsinger et al. 1984), and recent theory indicates that pollen discounting, along with other aspects of the dynamics of pollen transfer may be essential to the evolutionary stability of mixed mating (Johnston 1998, Morgan & Wilson 2005, Porcher & Lande 2005).

The mating system of cleistogamous species (used here to designate species in which individuals can produce both CH and CL) is not well described by models that emphasize the balance between inbreeding depression and the automatic fitness advantage. Because CL never reach anthesis, they cannot contribute any pollen to outcrossing and therefore do not reap the automatic fitness advantage (i.e., they suffer 100% pollen discounting). On the other hand, CL are typically considerably smaller and therefore cheaper to produce than CH (Lord 1981, Schemske 1978, Waller 1979) and can produce seed even when pollen vectors fail. The greater economy and reliability of CL provide advantages to selfing that do not occur in mixed mating species with monomorphic flowers. The other main genetic force in models of mating system evolution, inbreeding depression, is expected to be low in regularly selfing species (Husband & Schemske 1996), including cleistogamous taxa. The economy and reliability of CL combined with the expectation of low inbreeding depression suggest that once cleistogamy arises, complete selfing via CL should be favored. Because selection favoring selfing will be particularly strong in cleistogamous species, the forces that maintain outcrossing via the production of CH must be exceptionally pronounced. These features make cleistogamous species particularly favorable empirical systems for identifying factors that maintain the potential for outcrossing once selfing evolves. The relative ease of measuring costs and benefits of reproduction via CH and CL also facilitates quantitative estimation of the magnitude of selection necessary to maintain mixed mating in cleistogamous species, which could be used to evaluate the likelihood that specific mechanisms are sufficient to explain the maintenance of outcrossing in cleistogamous species.

Although theory for mating system evolution has typically treated cleistogamy as a special case, if at all (but see Lu 2002, Masuda et al. 2001, Schoen & Lloyd

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**Inbreeding depression:**

The reduction of fitness in selfed (relative to outcrossed) progeny

**Pollen discounting:**

Reduction in the amount of pollen available for outcrossing as a function of self-fertilization

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1984), the pronounced dimorphism associated with mating system in cleistogamous species has made them attractive subjects for empirical studies of the patterns and consequences of selfing and outcrossing (e.g., Clay & Antonovics 1985, Lu 2000, Schemske 1978, Schmitt & Gamble 1990, Waller 1979). Consequently, the literature contains quantitative data on relative costs of reproduction by the two flower morphs, the relative fitness of progeny produced by each flower type, CH outcrossing rates, and environmental factors associated with increased or decreased proportion of CL produced. The possible insight that cleistogamy could provide into mating system evolution appears to have been overlooked.

Here we summarize the theoretical and empirical literature on cleistogamous species that is relevant to mating system evolution and consider how cleistogamy might be further exploited as a tool in the study of the evolution of plant mating systems. We begin by summarizing the formal models and verbal arguments that have been advanced to explain the evolutionary stability of cleistogamy. We then review data from 60 empirical studies of cleistogamous species that are relevant to the predictions and assumptions of these models. Finally, we describe the evolutionary scenarios that appear most likely to account for the maintenance of outcrossing once selfing arises in cleistogamous species.

### Variations on the Theme of Cleistogamy

True cleistogamy was defined by Lord (1981) as the presence of two developmentally distinct flower types. CL are consistently characterized by reduction in the size of the androecium and by precocious maturation of anthers relative to CH of the same species (Lord 1981). Beyond these commonalities, there are many variations on the theme of cleistogamy.

The degree of morphological divergence of CH and CL can range from primarily a matter of differences in organ size as in *Lamium amplexicaule*, to substantial differences in organ shape as in *Viola odorata* (Lord & Hill 1987). In a number of species, seeds produced by the two flower types differ in size as well as in germination behavior (see e.g., McNamara & Quinn 1977, Zeide 1978). Some cleistogamous species are also amphicarpic, producing both underground seeds with limited dispersal potential and more readily dispersed above-ground seeds (Schnee & Waller 1986, Weiss 1980). Floral phenology of cleistogamous species ranges from simultaneous to sequential, nonoverlapping production of the two floral forms.

The degree of cleistogamy, measured as the proportion of flowers produced by an individual that are cleistogamous, varies both among and within species in relation to plant size and growing conditions (see e.g., Clay 1983, Le Corff 1993, Weiss 1980). Little is known about the genetic basis for variation in degree of cleistogamy in nonagricultural species, although Clay (1982) reported a broad sense heritability of 52.6% in the field and 71.6% in the greenhouse for percent CL for a population of the grass *Danthonia spicata*. Crosses between lines of the cultivated annual plant *Salpiglossis sinuata* that differ in degree of cleistogamy suggest that a dominant allele at a single major locus confers cleistogamy and that modifiers influence the degree of cleistogamy (Lee et al. 1976). Recent work with cultivated barley, *Hordeum vulgare*

spp. *vulgare*, suggests that two major genes control cleistogamy and that the direction of dominance is opposite for the two loci (Turuspekov et al. 2004).

Cleistogamy is particularly common among members of the grass family, Poaceae (Campbell et al. 1983), and in dicot families characterized by CH with pronounced adaptation for zoophily such as the Balsaminaceae, Fabaceae, and Violaceae (Lord 1981, Plitmann 1995). Herbaceous annuals and perennials are approximately equally represented among cleistogamous taxa, but few woody species are cleistogamous (Plitmann 1995).

## THEORIES FOR THE EVOLUTIONARY STABILITY OF CLEISTOGAMY

### Hypotheses for the Maintenance of Chasmogamous Flowers

Three mathematical models (Lu 2002, Masuda et al. 2001, Schoen & Lloyd 1984) have formally addressed the conditions that can favor maintenance of production of both CH and CL by individuals (**Table 1**). Schoen & Lloyd (1984) added the unique features of cleistogamy to the general modeling framework for the evolution of plant mating systems based on the balance between automatic selection and inbreeding depression. Schoen & Lloyd's model incorporates the relative costs of reproduction by the two flower types, the complete inability of CL to participate in outcrossing

**Table 1** Mathematical and verbal models proposed to maintain the production of both chasmogamous flowers (CH) and cleistogamous flowers (CL)

Model citation	Critical assumptions	Force proposed to maintain both CH and CL	Predictions for empirical data
Schoen & Lloyd 1984	Two environments, with parental fitness being maximized by a different flower type in each environment	Adaptive phenotypic plasticity	Each flower type produced under conditions in which it makes a greater contribution to parental fitness
Masuda et al. 2001	Pure chasmogamous flowering favored in the absence of geitonogamy, which increases with number of CH	Geitonogamy	Simultaneous production of CH and CL
Lu 2002	Selfing lineages purge lethal mutations, but different lines fix different, mildly deleterious alleles	Heterosis	Heterosis in crosses between lines that have undergone uninterrupted selfing
Waller 1980, Zeide 1978	Production of two flower morphs reduces variance in fitness over time	Variance discounting	Inverse relationship between plant size and fraction of flowers that are cleistogamous
Waller 1980, 1984; Schmitt & Ehrhardt 1987	Temporal variation in sibling density and less competition among sibling progeny of CH than among progeny of CL	Variance discounting	Greater fitness of progeny of CH than progeny of CL when grown in competition with siblings

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**Autogamy:**

Self-fertilization within a flower

**Geitonogamy:**

Self-fertilization between flowers on the same plant

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(i.e., 100% pollen discounting), and potential differences in the relative fitnesses of progeny derived from the two flower types, including both the effects of flower type per se (e.g., differences in seed size) and inbreeding depression. Initial analysis of the model suggests that a mutation resulting in the production of CL would be favored when costs of male function are high and/or the structure of CH limits reproductive assurance via autogamy. The correspondence of these conditions with the high frequency of cleistogamy in the grasses and in families with pronounced adaptation for zoophily suggest that the model does capture some of the essential features of cleistogamy.

Schoen & Lloyd (1984) used their model to compare the fitnesses of alternate phenotypes that differ only in their degree of cleistogamy (proportion of total flowers that are cleistogamous). Adding the details of cleistogamy alone produced the same conclusions as have general models for mating system evolution (e.g., Charlesworth & Charlesworth 1987, Lande & Schemske 1985, Lloyd 1979). Either complete cleistogamous selfing, or complete chasmogamous outcrossing was favored depending on the relative costs of chasmogamous and cleistogamous reproduction, the selfing rate of CH, and the relative viabilities of offspring produced via CL and CH.

The predictions were strikingly different when temporal variation in the environment of reproducing parental plants was added to the model (Schoen & Lloyd 1984). This version of the model assumes that during a portion of the flowering season, reproduction via CH contributes more to parental fitness than reproduction via CL and that the reverse is true under other conditions. The model predicts that a phenotype that is able to respond perfectly to an environmental cue by producing the appropriate flower type will have greater fitness than one that responds to a lesser extent, making temporally separated production of both CH and CL stable. This is implicitly a model of cleistogamy as adaptive phenotypic plasticity, which requires that selection favors different phenotypes (in this case flower types) in different environments. If there is only one selective environment, or if plants cannot detect and respond to a cue indicating which flower type is favored, production of both CH and CL would not be stable.

The model of cleistogamy as a form of adaptive plasticity is plausible, but relies on the presumed existence of alternate environmental states in which each floral morph is favored. Schoen & Lloyd (1984) suggested temporal variation in the availability of pollinators as one scenario that might impose such a pattern of selection. The production of CH would be favored when pollinators were active, and reproduction via CL would contribute more to parental fitness when they were scarce or absent. Schoen & Lloyd (1984) also explored a variant of their model that includes differential dispersal of seeds from CH and CL, but because this model has limited generality, we will not consider it further here.

Masuda et al. (2001) later added the effect of increased geitonogamous chasmogamous selfing (selfing between CH of the same individual) as a function of increased CH production to Schoen & Lloyd's framework. They implicitly imposed conditions that favor chasmogamous reproduction, and asked if an increase in geitonogamy with increased production of CH can stabilize the production of both CH and CL by limiting the advantages of producing only CH. The model predicts that the production

of both CH and CL can be stable, although it does not specify the conditions that favor the production of CH in the absence of geitonogamy. This model has several parallels among the models for mixed mating in species with monomorphic flowers that suggest that selfing persists in primarily outcrossing taxa as a byproduct of adaptations to increase pollinator attraction (e.g., Johnston 1998, Porcher & Lande 2005, Scofield & Schultz 2006). This scenario seems much less likely for cleistogamous species because CL would not contribute to pollinator attraction but would be expected to exact a cost owing to inbreeding depression, especially in a primarily outcrossing species. In addition, regular cleistogamous selfing would be expected to reduce inbreeding depression via purging and eventually shift selection toward complete selfing.

A distinctly different idea for the maintenance of both CH and CL has been suggested by Lu (2002) who proposed that the two floral morphs are maintained as a balance between the benefits of the economy of purging in CL and those of heterosis, which can only be realized via chasmogamous outcrossing. Lu reasons that CL provide an economical means of purging inbreeding depression caused by recessive lethals, but that uninterrupted selfing that would result from complete CL production could permit the fixation of more mildly deleterious mutations within selfing lineages. This load could be reduced by heterosis in crosses between serially selfed lines that have fixed different mutations, which requires the production of CH. Lu modified the fitness equations of the Schoen & Lloyd model to include effects of purging in CL and of heterosis for crosses between two parents, each of which was derived from cleistogamous seeds from a different selfing lineage. Her model suggests that if CL provide cheap purging of lethals and outcrossing confers heterosis, then as the selfing rate in a population increases, the benefit of crossing between lines also increases and that this force favors the maintenance of chasmogamous outcrossing. This model seems plausible, although the greater economy of CL alone might be sufficient to favor their production, even without their role in purging, leaving the potential for heterosis as the novel explanation for the maintenance of CH.

Several verbal hypotheses have advanced the idea that unpredictable variation in the environment periodically provides an advantage to reproduction via chasmogamous outcrossing that balances selection favoring the economy and reliability of reproduction via cleistogamous selfing (Waller 1980, Zeide 1978). In contrast to the suggestion of adaptive plastic response to predictable variation invoked by Schoen & Lloyd (1984), these explanations portray the production of both CH and CL as a variance discounting strategy (Real 1980, Seger & Brockmann 1987) that confers greater geometric mean fitness than either pure CH or CL when the environment varies unpredictably through time. The mechanisms that have been proposed to underlie the advantage of producing genetically variable progeny parallel mechanisms proposed to explain the maintenance of sexual reproduction.

Waller (1980, 1984) and Zeide (1978) suggest that although reproduction by CL is cheaper and more reliable, if there are periods of time during which CH are favored, then producing both flower types could reduce the long-term variance in fitness and therefore maximize geometric mean fitness. Because outcrossing in CH allows greater recombination than does self-fertilization, one possible mechanism favoring

chasmogamous reproduction is that the greater genetic variation generated by chasmogamous outcrossing could facilitate adaptation when the environment changes (Waller 1984). This scenario parallels the suggestion that the production of genetic variation via sexual reproduction allows adaptation to environmental change and favors the maintenance of sex (Kondrashov 1993, Maynard Smith 1978, Williams 1975).

Avoidance of sibling competition has also been invoked both to explain the advantage of chasmogamous reproduction (Waller 1980) and to favor the maintenance of sexual reproduction (Maynard Smith 1978, Price & Waser 1982, Williams 1975, Young 1981). The argument for cleistogamy is that half-sibs produced by chasmogamous outcrossing are genetically more dissimilar than full-sibs that result from cleistogamous selfing and are therefore expected to experience a smaller reduction in fitness when grown in competition with each other than would full-sib selfed offspring produced via CL. The production of both CH and CL would be favored by unpredictable temporal variation in the degree to which siblings experience competition. Periods of intense competition would favor chasmogamous reproduction, and times of reduced competition would favor cleistogamous reproduction for the sake of energetic economy.

### **Data Relevant to Evaluating Hypotheses for the Stability of Cleistogamy**

None of the models for the maintenance of production of both CH and CL has been tested directly, and the complete data necessary for such tests is not available in the literature. However, published empirical data on cleistogamous species can be used to evaluate the likelihood of the scenarios proposed by different models, to suggest what would constitute appropriate tests of these models and to determine the magnitude of the advantage that must be conferred by any mechanism proposed to maintain investment in CH despite their greater energetic cost and lower reliability.

The frequency and phenology of the production of CH and CL could illuminate the roles of adaptive plasticity and geitonogamy in the maintenance of cleistogamy. If mixed production of CH and CL constitutes adaptive plasticity (Schoen & Lloyd 1984), then each flower type should be produced in the environment in which it contributes most to parental fitness. If, for example, variation in pollinator availability selects for the production of CH and CL during different seasons, then CH and CL should be produced at different times and each during the season in which it is favored. Data on changes in the proportion of flowers that are CH in response to the environment could suggest what specific environmental factors favor CH reproduction. A decrease in the number of CH with total flower number would be consistent with avoidance of geitonogamy (Masuda et al. 2001) because the opportunity for geitonogamous pollination would be expected to increase with display size (see e.g., Barrett et al. 1994, Klinkhamer & de Jong 1993, Routley & Husband 2003). In contrast to the scenario for adaptive plasticity in response to seasonal variation in pollinator availability, avoidance of geitonogamy should favor simultaneous rather than sequential production of the two flower morphs.



The hypothesis that the production of both CH and CL reflects adaptation to an unpredictably varying environment is difficult to test empirically because demonstrating variance discounting requires a long temporal sequence of fitness estimates, but data on the degree of cleistogamy and on sibling competition can support or refute the mechanisms purported to underlie selection for mixed production of CH and CL in these models. Zeide (1978) suggested that individuals with limited resources should favor the production of the lower risk phenotype. Thus we might expect smaller plants and those in poorer condition to produce CL in preference to CH. The feasibility of the sibling competition mechanism would be supported by evidence of stronger competition among more related cleistogamous siblings than among less related outcrossed chasmogamous siblings.

Data on the frequency of fruit set of each flower type and on the energetic cost and relative performance of seeds produced by CH and CL can be combined to estimate the magnitude of advantage to CH necessary to justify their continued production. This estimate could serve as a benchmark to evaluate the likelihood that any particular mechanism is sufficient to account for the continued production of CH despite their greater energetic expense and reliance on pollen vectors. Dissection of the cost of CH into its component parts can also identify specific forces that are or are not likely to account for their maintenance.

## REVIEW OF THE EMPIRICAL DATA

We reviewed 60 published studies of cleistogamous species and summarized the data on the phenology of flower production, the identity of environmental factors associated with differences in the percent of flowers produced that are cleistogamous, and the relative fitness costs and benefits of reproduction via CH and CL, including the rate of selfing in CH and the magnitude of inbreeding depression.

### Phenology and Plasticity

We found 37 studies containing information on the timing of production of CH and CL and 18 describing plastic changes in degree of cleistogamy. We report these data by genus to correct for the disproportionately large representation of species within certain genera (e.g., *Impatiens*, *Oxalis*, and *Viola*). Unexpectedly, we found a difference in the phenology of flower dimorphism between annual and perennial cleistogamous taxa (**Supplemental Table 1**; follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>). For every annual species ( $N = 13$  species in 11 genera) for which we found data, there was overlap in the production of the two flower types, and these species always produced CL first (**Supplemental Table 1**), followed by simultaneous production of CH and CL, and occasionally a second period of only CL. Among perennials, about half of the species (total  $N = 17$  species in 10 genera) produced the two flower types sequentially in distinct seasons. Also unlike the annuals, most perennials initiated production of CL either simultaneously with or after the production of CH within a flowering season (**Supplemental Table 1**). In at least some perennial cleistogamous species



**Table 2** Estimates of the cost per seed for reproduction by cleistogamous flowers (CL) relative to that by chasmogamous flowers (CH); relative fertility (probability of fruit set) and relative flower cost represent two components of relative cost per seed<sup>a</sup>

Species (Family)	Relative fertility	Relative flower cost	Relative cost per seed	Reference
<i>Ampicarpum pursbii</i> (Poaceae)	4.89			McNamara & Quinn 1977
<i>Commelina benghalensis</i> (Commelinaceae)	1.11			Kaul et al. 2002
<i>Collomia grandiflora</i> (Polemoniaceae)		0.9		Wilken 1982
<i>Centaurea melitensis</i> (Asteraceae)	1.02			Porras & Alvarez 1999
<i>Impatiens capensis</i> (Balsaminaceae)	1.4	0.01	0.57	Schemske 1978, Waller 1979
<i>Impatiens pallida</i> (Balsaminaceae)	1.77	0.01	0.38	Schemske 1978
<i>Microlaena polynoda</i> (Poaceae)	4.26	0.78		Schoen 1984
<i>Oxalis acetosella</i> (Oxalidaceae)	1.25			Berg 2003
<i>Scutellaria indica</i> (Lamiaceae)	19.2	0.15		Sun 1999
<i>Viola birta</i> (Violaceae)	1.01			Berg 2003
<i>Viola mirabilis</i> (Violaceae)	1.08			Berg 2003
<i>Viola pubescens</i> (Violaceae)	0.43			Culley 2002
<i>Viola riviniana</i> (Violaceae)	0.99			Berg 2003
<i>Viola septemloba</i> (Violaceae)	1.43	0.44	0.67	A.A. Winn, unpublished data
Mean	3.06	0.38	0.54	
SD	5.02	0.39	0.15	

<sup>a</sup>All values are the ratio of CL to CH.

(Table 2). Complete data necessary to estimate the average cost of seed production via each flower type were available for three species and indicate that the cost of seed production via CL is slightly more than half the cost via CH (Table 2). Estimates of relative fertility (probability that a flower will successfully set fruit) of CH and CL were reported for 13 species, and on average, fertility of CL was 3.06 times that of CH (Table 2). Estimates of relative fertility varied widely, from 0.43 for *Viola pubescens* (Culley 2002), to 19.2 in *Scutellaria indica* (Sun 1999), but 11 of the 13 estimates were greater than or equal to 1, indicating that greater fertility of CH is probably rare. Although CH were as much as 100 times more energetically costly to produce, the cost of a flower is typically not a large proportion of the total cost per seed, less than 1% for CL and approximately 10% for CH in *Impatiens capensis*, for example (Schemske 1978). Consequently, flower cost alone contributed very little compared with fertility cost to differences in the energetic cost of seed production by CH and CL.

The fitness of progeny produced via CL is often equivalent to if not greater than the fitness of progeny produced via CH (Supplemental Table 3). The average fitness of CL relative to CH progeny for 19 studies of 14 cleistogamous species was 1.12 (standard deviation 0.43) (Supplemental Table 3). This is a rough approximation because many estimates are based on a limited portion of the life cycle (e.g., seed germination or early growth only) and/or were obtained from individuals grown

in artificial conditions (e.g., greenhouse), which may not accurately reflect fitness differences that accrue under natural conditions (cf. Armbruster & Reed 2005).

Both differences in nongenetic phenotypic characteristics of seeds produced by CH and CL (e.g., maternally controlled differences in size, dispersal potential, and germination behavior) and inbreeding depression can contribute to differences in the fitness of chasmogamous and cleistogamous progeny. Studies comparing open-pollinated chasmogamous progeny with progeny from CL are appropriate for determining the contributions of reproduction by each flower type to parental fitness, but estimates of inbreeding depression could be used to partition this difference into effects owing to nongenetic differences in seed traits produced by CH and CL and those owing to differences in the genetic make-up of seeds from CH and CL. We found only three estimates of the relative fitness of progeny from hand outcrossed and selfed CH, which are not confounded by nongenetic differences in seed phenotype or by selfing in CH. Culley (2000) reported inbreeding depression  $[1 - (W_{\text{CH selfed}}/W_{\text{CH outcrossed}})]$  of 10% in *Viola pubescens* (this estimate excludes differences in percent germination, which was unusually low and considerably greater for seeds produced by selfing than those produced by outcrossing). Studies of *Impatiens capensis* (Lu 2002) and *Viola septemloba* (C.G. Oakley & A.A. Winn, submitted) estimated inbreeding depression of 22% and 43%, respectively.

Self-fertilization of CH could reduce the genetic advantage that CH progeny are expected to enjoy. Selfing rates of CH have been reported in five studies, three of which present estimates for *Impatiens capensis*. The overall average is 50% (standard deviation 28%), with estimates ranging from 25% to 48% in *Impatiens capensis* (Lu 2000, Mitchell-Olds & Waller 1985, Waller & Knight 1989) to 36% in *Viola* (Culley 2002), to greater than 96% in *Lespedeza capitata* (Cole & Biesboer 1992). Because estimates of selfing we report are for CH only, and all CL are selfing, total selfing rates of cleistogamous species are likely to be high. For example, the selfing rate in CH of *Viola pubescens* was estimated to be 36% (Culley 2002), but 55% of the flowers produced are cleistogamous, so the total selfing rate would approach 71%.

### How Strong Must Selection for Outcrossing be?

We can estimate the magnitude of the fitness advantage to cleistogamous reproduction relative to chasmogamous reproduction by dividing the estimates of the relative fitness of cleistogamous progeny by the estimates of the relative cost per seed of cleistogamous reproduction (see **Figure 1**). Complete data are available for two species and indicate a fitness advantage to cleistogamous reproduction of 15% for *Impatiens capensis* and of 231% for *Viola septemloba*. In other words, after accounting for differences in energetic cost of production and for differences in progeny fitness including inbreeding depression, some evolutionary force must provide an advantage to reproduction by CH of some magnitude to favor their continued production.

We also estimated a composite average relative advantage of cleistogamous reproduction using an average of the costs and benefits of reproduction via each flower type over all species for which we found data on fertility of CH and CL (**Table 2**) or the fitness of progeny from CH and CL (**Supplementary Table 3**). This composite

estimate assumes that the combined weight of flowers, fruits, and seeds is similar for reproduction via CH and CL, and that seed number per fruit is likewise similar. Given these assumptions, some evolutionary force must provide an advantage to CH greater than 342% that of CL reproduction to justify their continued production. This value is 193% if the extreme differential fertility reported for *Scutellaria indica* (Table 2) is ignored.

Although the accuracy of the estimated fitness advantage of reproduction via cleistogamy might be improved by more data on the relative energetic costs of CH and CL (which would probably raise the estimate) and more complete estimates of inbreeding depression (which might increase or decrease it), much of the estimated cost of chasmogamous reproduction derives from differences in the economy and reliability of seed production, for which data were reasonably abundant and accurate.

## EVALUATION OF THE HYPOTHESES

Collectively, the empirical data from studies of cleistogamous species show that on average, CL are cheaper to produce, have greater fruit set (Table 2), and produce progeny that suffer little, if any, reduction in fitness relative to progeny of CH (Supplemental Table 3). High overall rates of selfing and low estimates of inbreeding depression suggest that cleistogamous species can effectively purge inbreeding depression via selfing in CL. After accounting for differences in energetic costs of production and for differential progeny fitness, chasmogamous reproduction must repay a fitness cost of between 15% and 342% of the benefit of cleistogamous reproduction to parental fitness to prevent evolutionary replacement by pure CL. The majority of the advantage to CL appears to derive from their greater likelihood of setting fruit rather than the lower energetic cost of individual CL.

The empirical data provide some circumstantial support for each of the proposed mechanisms for the evolutionary stability of producing both flower forms. However, most of these mechanisms appear to be either unlikely to explain the persistence of CH and/or unable to generate the magnitude of selection necessary to counter the advantage of CL flowers that we detected.

Sequential, temporally separated production of CH and CL, reported for some perennials (Supplemental Table 1), is consistent with adaptive plastic response to seasonal variation in factors that influence the relative benefits of reproduction via the two flower types. However, this interpretation rests on the assumption that there are environmental states in which each flower morph contributes more to parental fitness than the alternative, which has not been demonstrated for CH. Schoen & Lloyd (1984) suggested that chasmogamous flower production might be favored when pollinators were abundant and cleistogamous flower production favored when they were scarce or absent but, given that CL do not require pollinators to set seed, are energetically cheaper to produce, and suffer little if at all from the effects of inbreeding depression, it is difficult to envision why CL should not be produced in all environments. Adaptive phenotypic plasticity might in principle produce strong selection favoring the ability to produce alternate phenotypes (Via & Lande 1985), but unless conditions that favor

reproduction via CH over CL can be identified, the Schoen & Lloyd model cannot explain the stable persistence of the two flower forms.

We suggested at the outset that the hypothesis of avoiding geitonogamy (Masuda et al. 2001) was an unlikely candidate for explaining the stability of cleistogamy. Although simultaneous production of CH and CL in many species (**Supplemental Table 1**) is consistent with the hypothesis that avoiding geitonogamy contributes to the maintenance of cleistogamy, two other patterns do not fit the geitonogamy scenario. The plastic decrease in proportion of CL with increasing plant size (**Supplemental Table 2**) runs counter to the expectation that avoiding geitonogamy would become more important as plant size, and presumably total number of flowers, increases (Barrett et al. 1994, Klinkhamer & de Jong 1993, Routley & Husband 2003). The apparent priority of the production of CL observed in all annuals and at least some perennials also conflicts with the geitonogamy hypothesis.

We were not able to address the hypothesis that heterosis could maintain selection for CH as suggested by Lu (2002), because we found no data on the fitness of crosses between inbred lines relative to crosses between outbred lines. Nearly all the data on the costs and benefits of the production of the two flower types support selection favoring CL, supporting our suggestion that purging per se is not required for Lu's hypothesis. The available data on inbreeding depression in cleistogamous species is not informative with respect to heterosis because we do not know the inbreeding histories of the parents of the crosses.

As expected, we found no estimates of geometric mean fitness as a function of degree of cleistogamy, which would be necessary for a direct test of the variance discounting hypothesis for the maintenance of cleistogamy. The common pattern of a plastic decrease in the degree of cleistogamy with increasing plant size and resource availability (**Supplementary Table 2**) suggests that chasmogamous flower production is relatively more advantageous under conditions that are favorable for growth. Although this pattern could be interpreted as support for an adaptive plastic response to spatial environmental variation in conditions affecting the fitness benefits of reproduction via CH and CL, such a scenario seems likely to select for a response resulting in either all CL or all CH within each environment rather than a mixture. We concur with Waller (1980) who noted that a plastic increase in the proportion of CH with plant size or environmental favorability is consistent with risk averse variance discounting, although it is only circumstantial support.

Several studies provided data necessary to test the assumption of greater effects of competition among siblings derived from CL than from CH, which is required for avoidance of sibling competition to explain the stability of mixed chasmogamous and cleistogamous reproduction. Chasmogamously derived half-siblings grown in competition did not outperform CL derived full-siblings grown in competition in any of five tests of four different species (Berg & Redbo-Torstensson 1999, 2000; McCall et al. 1989; Schmitt & Ehrhardt 1987; Schmitt et al. 1985). Additional data from noncleistogamous species also provide little support for this hypothesis. In a general review of 22 studies of plants and insects that compared competition between similar and dissimilar genotypes, Price & Waser (1982) reported an average 3% advantage of dissimilar genotypes compared to similar genotypes. Additional subsequent studies

have reported either that siblings grown in competition outperformed nonsiblings grown in competition (Donohue 2003, Tonsor 1989), or that there was no detectable difference (Willson et al. 1987; but see Kelley 1989, Schmitt & Antonovics 1986). An average advantage of 3% is much too weak relative to the chasmogamous advantage required (1.15- to 3.42-fold) to support sibling competition as a general explanation for the maintenance of CH.

## SYNTHESIS AND PROSPECTUS

Evaluation of the assumptions and predictions of hypothesis for the stability of cleistogamy with published data suggests that adaptive plasticity, avoidance of geitonogamy, and avoidance of sibling competition are unlikely to explain the evolutionary stability of mixed mating in cleistogamous species. Although other mechanisms of variance discounting and/or heterosis might contribute to the maintenance of outcrossing in cleistogamous species, additional forces that have not been included in models of cleistogamy might also be relevant. In particular, more recent general models for the evolution of mixed mating find that the dynamics of pollen transfer may be critical to understanding the stability of mixed mating (Holsinger 1991, Johnston 1998, Porcher & Lande 2005), and they may also play a role in maintaining cleistogamy.

### Candidates for the Maintenance of Cleistogamy

Chasmogamous flowers can perform two functions that CL cannot; they can produce outcrossed offspring, which experience a greater degree of genetic recombination than selfed offspring, and they can contribute to male fitness by siring seeds produced by different individuals. The question raised by our review of the data for cleistogamous species is, What forces related to these two functions could be of large enough magnitude (either alone or in concert) to repay the 15–342% fitness cost of the more expensive and less reliable seed production of CH? Two candidates are pollen dynamics and heterosis in outcrossing between inbred lines.

A recent model of mating system evolution suggests that genetic forces acting on mating system and many aspects of pollination ecology combine to prevent the evolution of complete self-fertilization (Porcher & Lande 2005; cf. Holsinger 1991, Johnston 1998). The model predicts that when the selfing rate is very high, the joint effects of pollen limitation, pollen discounting, and inbreeding depression combine to generate selection preventing further increase in the selfing rate. The magnitude of selection that can be generated by this scenario is not known, but it might be exaggerated in cleistogamous species because it would need to counter exceptionally strong selection favoring the economy and reliability of selfing via CL. The model could be modified to account for the unusual features of cleistogamy and parameterized with data from a particular species to determine the likelihood that this force could maintain the observed investment in CH.

The role of heterosis in favoring the maintenance of CH in Lu's model invokes a scenario similar to that portrayed by models of metapopulation genetics. Several

models of metapopulation genetics support the potential for rare gene flow between populations to lead to substantial heterosis (Roze & Rousset 2004, Theodorou & Couvet 2002, Whitlock et al. 2000), especially for small, predominantly selfing populations. Crosses between populations may result in heterosis because a portion of the genetic load may become fixed within populations owing to drift. Drift is expected to fix alternate alleles in different populations, such that crosses between populations can mask previously expressed deleterious mutations (Roze & Rousset 2004, Theodorou & Couvet 2002, Whitlock et al. 2000). Empirical evidence of substantial heterosis in interpopulation crosses (e.g., Fenster 1991, Fenster & Galloway 2000, Paland & Schmid 2003, van Treuren et al. 1993, Weller et al. 2005) is consistent with this theory and supports a potentially large advantage to maintaining the potential for periodic outcrossing.

In some respects, Lu's model depicts an extreme metapopulation in which high rates of selfing via CL generate selfing lineages, each with an effective population size of one, within a larger population. These selfing lineages can build up a genetic load that can only be relieved by outcrossing. Although the heterosis resulting from crosses between inbred lines may need to be large to justify the expense of CH in cleistogamous species, this mechanism could also operate in species with monomorphic flowers whenever selfing rates are high enough to create the appropriate genetic structure. A first step in determining whether this scenario is plausible would be to determine how much load accumulates in selfing lineages. Studies in noncleistogamous species have shown that uninterrupted selfing over 5 to 6 generations can build up substantial load as revealed by crosses between selfing lines (Barrett & Charlesworth 1991, Dudash et al. 1997; cf. Johansen-Morris & Latta 2006).

### Additional Approaches to the Study of Cleistogamy

The mechanisms that favor the maintenance of CH in cleistogamous species are also likely to operate in mixed mating species with monomorphic flowers. Because the proposed effects of these mechanisms are likely to be more pronounced in cleistogamous taxa, these species may provide particularly suitable systems in which to pursue the empirical work necessary to test their feasibility and likely relative importance. Considerable existing data on the fitness costs and benefits of reproduction via CL and CH available for species of *Impatiens* and *Viola* make them particularly suitable for obtaining the additional data needed to determine which of the proposed mechanisms could be of sufficient magnitude to justify the continued production of outcrossing flowers. The additional data needed include estimates of fitness accrued by siring outcrossed progeny and the rates of evolution of inbreeding depression and fixed mutational load in natural populations.

A potentially valuable empirical approach that has not yet been pursued in cleistogamous taxa is the comparison of closely related species that differ in their degree of cleistogamy. A comparative approach could permit more focused, testable predictions about what factors are important for the evolution or maintenance of cleistogamy in a given taxonomic group. Culley & Klooster (2007) recently mapped the incidence of cleistogamy onto a composite phylogeny for the angiosperms. They identified several



possible instances of evolutionary loss of CL. Scrutiny of the factors associated with such losses may be valuable for identifying the conditions that favor the maintenance of CH.

Cleistogamous species present an interesting evolutionary enigma in their own right, but can also contribute to resolving the longstanding question of what maintains mixed mating in general and especially what maintains outcrossing once effective selfing evolves. General features of cleistogamous species are consistent with the current view that the forces of inbreeding depression and automatic selection alone are not sufficient to explain the stability of mixed mating. The relative ease with which the fitness consequences of reproduction via selfing and outcrossing can be quantified provides a yardstick for evaluating which of the many additional forces that have been proposed are most likely to play a role in the maintenance of mixed mating. Rather than making them arcane exceptions to mating system theory, many of the unusual features of cleistogamous species make them valuable tools for elucidating the adaptive significance of mixed mating.

## DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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## Errata

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