

An ESS model for the mixed production of cleistogamous and chasmogamous flowers in a facultative cleistogamous plant

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ABSTRACT

We have developed resource allocation models for the evolution of a mixed production of cleistogamous and chasmogamous flowers. The basic model takes into account the features associated with cleistogamous self-pollination (e.g. the greater economy and assurance of cleistogamous fertilization) and the inability of cleistogamous flowers to contribute to the outcrossed pollen pool. The basic model predicts that only one of each strategy (i.e. chasmogamy or cleistogamy) is favoured. However, when seasonal fluctuation of the fruit-to-flower ratio of chasmogamous flowers is considered, an evolutionarily stable strategy favours either cleistogamous or chasmogamous flower production. This fluctuation in fertility may explain the seasonally discrete production of dimorphic flowers in natural populations of some facultative cleistogamous plants. The simultaneous production of both of the dimorphic flowers is explained only when the effect of geitonogamous selfing of chasmogamous flowers is included in the model.

Keywords: chasmogamy, evolutionarily stable strategy, facultative cleistogamy, geitonogamy, resource allocation model, seasonal variation.

INTRODUCTION

Cleistogamy is a structurally modified mode of autogamy, in that the flowers never open and self-pollination occurs in a bud. Cleistogamous flowers have no nectar and no odour, their petals are either rudimentary or completely missing, and their stamens are often reduced in both number and size. In addition, cleistogamous flowers possess few pollen grains and the pistil is reduced in size (Darwin, 1877; Goebel, 1904; Ritzerow, 1908; Campbell *et al.*, 1983; Ellstrand *et al.*, 1984; Ruiz de Clavijo and Jimenez, 1993). This mode of reproduction is quite widespread and has been reported in 287 species from 56 angiosperm families (Lord, 1981).

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'True cleistogamy', as defined by Lord (1981), occurs when an individual plant produces both chasmogamous (opened and potentially cross-pollinated) flowers and cleistogamous flowers. The evolution of this type of cleistogamy is examined here; it will be referred to simply as cleistogamy, an example of typical multiple strategies (Lloyd, 1984).

The conditions under which cleistogamy is favoured were studied theoretically by Schoen and Lloyd (1984). In their 'near and far dispersal model', cleistogamy can be an evolutionarily stable strategy (ESS) if progeny from cleistogamous flowers have a higher viability near the parents than chasmogamous flowers. In the model, they assume that the seeds from chasmogamous flowers disperse further than those from cleistogamous flowers. Iwasa (1990) and Matsuda and Harada (1990) made similar predictions of the different theoretical schemes. These models apply well to a particular kind of cleistogamy known as 'geocarpy', in which cleistogamous seeds are dispersed underground only near their maternal parents (Zeide, 1978; Schnee and Waller, 1986; Schmitt and Gamble, 1990; Cheplick, 1994).

It is unclear, however, whether the near and far dispersal model can be applied to types of cleistogamy other than geocarpy. In the cleistogamous species, *Viola hondoensis*, the dispersal distance is not significantly different between cleistogamous and chasmogamous seeds (Masuda and Yahara, 1992). On the other hand, some populations of *Impatiens noli-tangere* produce only cleistogamous flowers early in summer and switch to produce only chasmogamous flowers late in summer (Masuda and Yahara, 1994). This phenomenon cannot be explained by the near and far dispersal model. Thus, the conditions under which facultative cleistogamy is favoured remain unclear.

The aim of this study was to develop a new ESS model that can be applied to other types of cleistogamy, not just geocarpy. First, we consider the features associated with cleistogamous self-pollination (e.g. the greater economy and assurance of cleistogamous fertilization, and the inability of cleistogamous flowers to contribute to the outcrossed pollen pool). Then, we consider variation in chasmogamous flower fertility, since Lloyd (1984) showed that seasonal change in the fitness component could favour multiple strategies. In addition, Masuda and Yahara (1994) and Berg and Redbo-Torstensson (1998) showed that chasmogamous flower fertility varies following seasonal changes in pollinator and resource availability in *Impatiens noli-tangere* and *Oxalis acetosella*, respectively.

Geitonogamy, the transfer of pollen among flowers on the same individual, results in the production of inbred seeds that suffer from inbreeding depression (Grant, 1975; Levin, 1984; Geber, 1985). In general, the rate of geitonogamy increases with the number of opened flowers per individual (Crawford, 1984; Geber, 1985; Hessing, 1988; Dudash, 1991; de Jong *et al.*, 1992; Klinkhamer and de Jong, 1993; Harder and Barrett, 1995). The increase in geitonogamous selfing reduces the benefit of chasmogamous flowers due to inbreeding depression, and could result in an ESS floral dimorphism. In this study, we incorporated the effect of geitonogamy in chasmogamous flowers into the model. In modelling, we intend to define parameters measurable for field populations.

THE MODEL

Basic model

We assume that two phenotypes, Ph (mutant) and Ph^* (wild type), co-occur in a population and differ only in the proportion of reproductive resources allocated to chasmogamous

and cleistogamous flower reproduction. We also assume that only same-size plants exist in the model. The phenotype Ph^* produces x^* chasmogamous flowers and y^* cleistogamous flowers; the phenotype Ph produces x chasmogamous flowers and y cleistogamous flowers. We assume that reproduction by chasmogamous and cleistogamous flowers is primarily constrained by nitrogen, water and light, so the total reproductive investment is limited. The parameters considered for the fitness of phenotype Ph are given in Table 1.

The phenotype Ph can transmit its genes via the following four pathways:

- through the mutant’s female function of outcrossed chasmogamous flowers;
- through the mutant’s male function of outcrossed chasmogamous flowers;
- through the mutant’s selfing of chasmogamous flowers, i.e. geitonogamy;
- through the mutant’s selfing of cleistogamous flowers.

After the four components are summed, the fitness of a mutant (W) is:

$$W = \frac{1}{2}(1-g)apx + \frac{1}{2}(1-g)apx \frac{(n-1)x^*}{x+(n-1)x^*} + g(1-d)apx + b(1-d)y \tag{1}$$

Here we assume that cleistogamous flowers produce a full complement of seed (i.e. the fertility of cleistogamous flowers is 1.0).

The total resources available for reproduction (R) are limited because we assume all plants are of the same size. Resources are used via two pathways: (1) through the chasmogamous flowers and fruits, and (2) through the cleistogamous flowers and fruits. The following equation holds:

$$R = (F_{CH} + pr_{CH})x + (F_{CL} + r_{CL})y \tag{2}$$

Table 1. Definitions of parameters

Parameter	Definition
x^*	number of chasmogamous flowers (wild type)
x	number of chasmogamous flowers (mutant)
y^*	number of cleistogamous flowers (wild type)
y	number of cleistogamous flowers (mutant)
F_{CH}	unit cost of a chasmogamous flower
F_{CL}	unit cost of a cleistogamous flower
r_{CH}	unit cost of a chasmogamous fruit
r_{CL}	unit cost of a cleistogamous fruit
R	total resources available for reproduction
m	genotypic correlation between outcrossed gametes; $0 \leq m \leq 1$
g	fraction of geitonogamous self-fertilization among chasmogamous flowers; $0 \leq g \leq 1$
a	number of chasmogamous seeds per fruit
b	number of cleistogamous seeds per fruit
p	fertility of chasmogamous flowers; $0 \leq p \leq 1$
n	number of individuals in the population
d	inbreeding depression; $0 \leq d \leq 1$
c	a constant of geitonogamy ($g = cx$) when $0 < x < 1/c$, where c is a constant value ($0 \leq c \leq 1$)

This means that the investment to x and y cannot increase infinitely. In a sufficiently large population, the fate of a mutant, Ph , which alters x^* to x can be examined by differentiating equation (1) by x , and by substituting x by x^* under the constraint of equation (2). From equation (1),

$$\frac{\partial W}{\partial x_{x=x^*}} = (1 - dg)ap + b(1 - d) \frac{\partial y}{\partial x} \quad (n \rightarrow \infty) \quad (3)$$

Here, $\partial y/\partial x < 0$ because the number of cleistogamous flowers (y) decreases with the number of chasmogamous flowers (x) based on the assumption of resource limitation. If $\partial W/\partial x > 0$, mutants that increase x are favoured. As a result of successive invasions of mutants increasing x , obligatory chasmogamous flowers evolve in equilibrium. If, however, $\partial W/\partial x < 0$, mutants that decrease x are favoured and obligatory cleistogamous flowers evolve in equilibrium. Facultative cleistogamous flowers are favoured only when $\partial W/\partial x = 0$ in the model. Under equation (3), however, this state would not be stable, because fluctuations in any of the seven parameters on the right-hand side of equation (3) would easily increase or decrease the marginal fitness value.

Model incorporating covariation of geitonogamous selfing rate with chasmogamous flower production in a cleistogamous plant

Next, we incorporate the effect of geitonogamous selfing of chasmogamous flowers into the basic model. In many plant species, the rate of geitonogamy increases with the number of opened flowers per individual (Crawford, 1984; Geber, 1985; Hessing, 1988; Dudash, 1991; de Jong *et al.*, 1992; Klinkhamer and de Jong, 1993; Harder and Barrett, 1995). Thus we assume that the geitonogamous selfing rate increases monotonically with the number of chasmogamous flowers (i.e. $g = cx$) when $0 < x < 1/c$, where c is a constant value ($0 \leq c \leq 1$). The fitness of Ph is given as

$$W = \frac{1}{2}(1 - g)apx + \frac{1}{2}x \frac{(1 - g^*)ap(n - 1)x^*}{x + (n - 1)x^*} + g(1 - d)apx + b(1 - d)y \quad (4)$$

where g^* is the geitonogamous selfing rate of phenotype Ph^* (wild type). When the population size n is large,

$$\begin{aligned} W &= \frac{1}{2}(1 - g)apx + \frac{1}{2}(1 - g^*)apx + g(1 - d)apx + b(1 - d)y \\ &= \frac{1}{2}(1 - cx)apx + \frac{1}{2}(1 - cx^*)apx + (1 - d)acpx^2 + b(1 - d)y \end{aligned} \quad (5)$$

Then, the marginal fitness is calculated by differentiating equation (5) by x , and substituting x with x^* :

$$\frac{\partial W}{\partial x_{x=x^*}} = ap + \frac{1}{2}(1 - 4d)acpx^* + b(1 - d) \frac{\partial y}{\partial x} \quad (6)$$

This marginal fitness increases or decreases monotonically as x^* increases, depending on the slope $\frac{1}{2}(1 - 4d)cap$.

When $x > 1/c$,

$$\frac{\partial W}{\partial x} = (1 - d)ap + b(1 - d) \frac{\partial y}{\partial x} \tag{7}$$

This is a constant value.

RESULTS

Basic model

Since the fertility of chasmogamous flowers (p) is very changeable due to pollinator availability and limited resources throughout the flowering season, we consider the relationship between p and the marginal fitness $\partial W/\partial x$. Three cases of the marginal fitness are recognized (Fig. 1). If the parameter of inbreeding depression (d) is very large, the marginal fitness is positive even with a low fertility of chasmogamous flowers (Fig. 1a), indicating that the mutations resulting in an increase in x are almost always favoured. As a result of successive invasions of mutants with an increased x , only obligatory chasmogamy is an ESS. If inbreeding depression is not severe and $\partial W/\partial x < 0$ is constant, then the mutations that decrease x are favoured, and only obligatory cleistogamy is an ESS (Fig. 1c). Facultative cleistogamy is favoured only when the fertility of the chasmogamous flowers varies (Fig. 1b). When p is above the critical value, the strategy setting chasmogamous flowers is an ESS, and vice versa. If p varies widely throughout a reproductive season, individuals may have only chasmogamous flowers at one time and only cleistogamous flowers at another time within the same season. Throughout the reproductive season, individuals set both types of flowers.

Model incorporating covariation of geitonogamous selfing rate with chasmogamous flower production in a cleistogamous plant

By incorporating the effect of geitonogamy into the model, we found six distinguishable cases that result in a change in marginal fitness, depending on d , X and Y (Fig. 2a–f). When

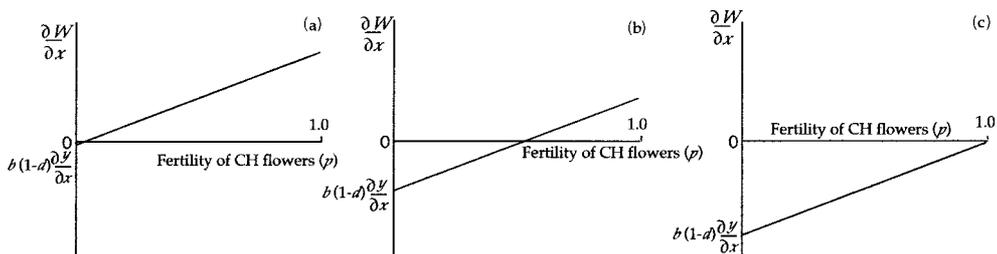


Fig. 1. Schematic representation of the relationship between marginal fitness ($\partial W/\partial x$) and the fertility of chasmogamous (CH) flowers. (a) Marginal fitness ($\partial W/\partial x$) is always > 0 ; (b) marginal fitness is positive when the fertility of chasmogamous flowers is high and is negative when the fertility of chasmogamous flowers is low; (c) marginal fitness is always < 0 .

the marginal fitness at $x^* = 0$ is designated Y and the marginal fitness at $x^* = 1/c$ is designated X , these six cases are: (i) $d > 1/4$, $Y > 0$ and $X > 0$ (Fig. 2a); (ii) $d > 1/4$, $Y > 0$ and $X < 0$ (Fig. 2b); (iii) $d > 1/4$, $Y < 0$ and $X < 0$ (Fig. 2c); (iv) $d < 1/4$, $Y > 0$ (Fig. 2d); (v) $d < 1/4$, $Y < 0$ and $X > 0$ (Fig. 2e); and (vi) $d < 1/4$, $Y < 0$ and $X < 0$ (Fig. 2f). In cases (i) and (iv), the marginal fitness remains positive, irrespective of x^* . Here the advantage of outcrossing is larger than that of selfing. By contrast, marginal fitness is always negative in cases (iii) and (vi). Here, the advantage of selfing is significantly larger than that of outcrossing. On the other hand, marginal fitness switches from negative to positive, or vice versa, in cases (ii) and (v).

The model provides specific predictions of the ESS resource allocation pattern (Fig. 3). Total reproductive investment will be allocated to chasmogamous flowers only in cases (i) and (iv) (Fig. 3a), and to cleistogamous flowers only in cases (iii) and (vi) (Fig. 3c). In case (ii), the total reproductive investment will be allocated to chasmogamous flowers only below the critical value; the allocation to chasmogamous flowers becomes constant beyond this value (Fig. 3b). Allocation to cleistogamous flowers begins at the critical value and increases monotonically with the total reproductive investment. In contrast to case (ii), the initial investment will be allocated to cleistogamous flowers; allocation to chasmogamous flowers begins at the critical value in case (iv) (Fig. 3d). Here, case (v) is in agreement with, and case (ii) is opposed to, the prediction of the near and far dispersal model (Schoen and Lloyd, 1984; Iwasa, 1990), because this model predicts that allocation to cleistogamous

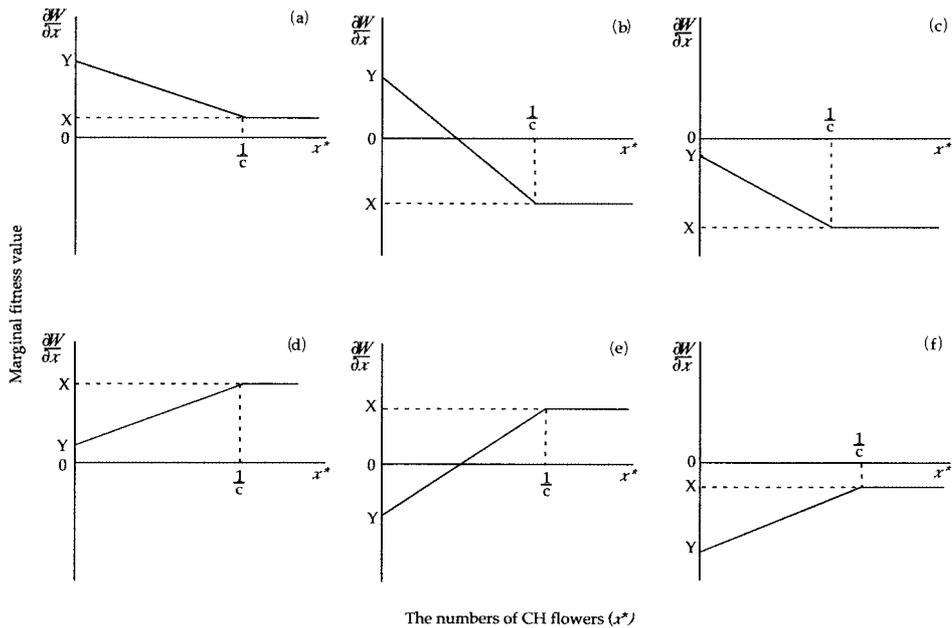


Fig. 2. The six cases of the relationship between marginal fitness ($\partial W/\partial x$) and geitonogamous selfing rate in chasmogamous (CH) flowers. (a) $d > 1/4$, $Y > 0$ and $X > 0$; (b) $d > 1/4$, $Y > 0$ and $X < 0$; (c) $d > 1/4$, $Y < 0$ and $X < 0$; (d) $d < 1/4$, $Y > 0$; (e) $d < 1/4$, $Y < 0$ and $X > 0$; (f) $d < 1/4$, $Y < 0$ and $X < 0$, where d is inbreeding depression and c is a constant about geitonogamy rate.

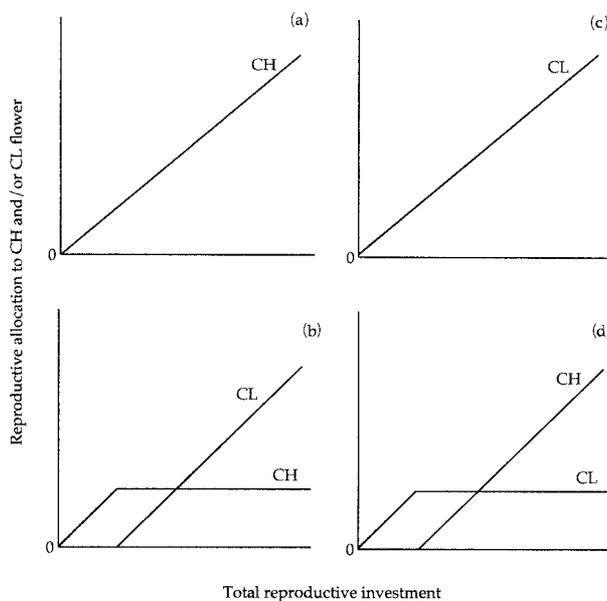


Fig. 3. The four cases of the relationship between total reproductive investment and the reproductive allocation to chasmogamy (CH) and/or cleistogamy (CL).

reproduction is constant, whereas allocation to chasmogamous flowers increases with total reproductive resources. By observing patterns of reproductive allocation in natural populations, it is possible to test which model is appropriate to explain the evolution of facultative cleistogamy.

Even when geitonogamous selfing rate does not increase monotonically with flower number, we could obtain similar but simpler results than under an assumption of linearity. For example, when $g = 1 - c/x$ ($c = \text{constant}$), the marginal fitness ($\partial W/\partial x$) is $apc/2x^* + (1-d)ap + b(1-d)\partial y/\partial x$. In this case, two distinguishable cases of the change in the marginal fitness were found (Fig. 4a,b), depending on $K = (1-d)ap + b(1-d)\partial y/\partial x$. Total reproductive investment will be allocated to chasmogamy alone when $K \geq 0$ (Fig. 4c). When $K < 0$, total reproductive investment will be allocated to chasmogamy alone below the critical value; allocation to chasmogamy is constant beyond this value (Fig. 4d).

DISCUSSION

The basic resource allocation model in this study predicts an alternative equilibrium of either obligatory chasmogamy or cleistogamy, as the model proposed by Schoen and Lloyd (1984) predicts. Thus, the basic model is insufficient to explain the evolution of facultative cleistogamy producing both types of dimorphic flowers. However, by altering the values of the parameters, especially the fertility of chasmogamous flowers, the evolutionary condition of dimorphic flower production becomes apparent.

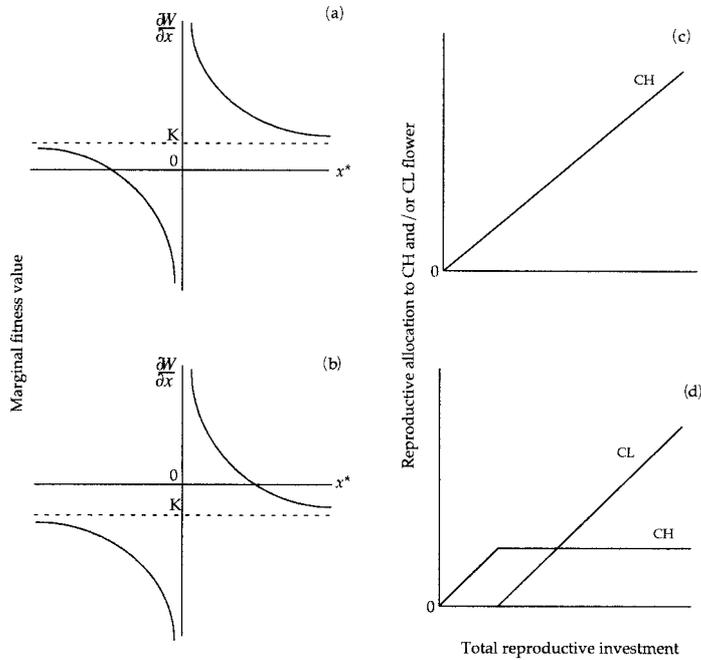


Fig. 4. ESS reproductive allocation to chasmogamy (CH) and/or cleistogamy (CL) under the assumption of the non-linearity relation between geitonogamous selfing rate and flower production. (a) $K \geq 0$, (b) $K < 0$, where $K = (1 - d)ap + b(1 - d) \partial y / \partial x$.

Seasonal variation

Equation (3) demonstrates that the marginal fitness of a mutant with an increased chasmogamous flower production varies with the fertility of the chasmogamous flowers (p), which may vary during a reproductive season (e.g. Masuda and Yahara, 1994; Berg and Redbo-Torstensson, 1998). Figure 1 shows the relationship between p and the marginal fitness. Under a combination of parameter values when p is very low, marginal fitness is negative and only cleistogamous flower production is favoured. By contrast, when p exceeds a critical value, only chasmogamous flower production is favoured. The changing seasonal strategy of switching cleistogamous or chasmogamous flower production can be explained as an adaptation to the seasonal variation in chasmogamous flower fertility.

This prediction explains the empirical observation of previous studies. Masuda and Yahara (1994) reported that some populations of *Impatiens noli-tangere* produce only cleistogamous flowers in early summer and produce only chasmogamous flowers in late summer. The fertility of chasmogamous flowers was approximately zero at the beginning of the flowering season. Therefore, the production of cleistogamous flowers only could be an ESS in *I. noli-tangere* in early summer. By contrast, at the middle and end of the flowering season, the fertility of chasmogamous flowers increases and the marginal fitness becomes positive, resulting in the production of predominantly chasmogamous flowers. The fluctuation in chasmogamous flower fertility in *I. noli-tangere* is probably

due to the temporal variation in pollinator activity (Masuda and Yahara, 1994). Similarly, Berg and Redbo-Torstensson (1998) reported that *Oxalis acetosella* produces chasmogamous flowers at the beginning of the flowering season and switches to cleistogamous flower production later. In addition, Berg and Redbo-Torstensson (1998) revealed that, in *Oxalis acetosella*, ramets with one or more chasmogamous flowers left fertilized generally produce more cleistogamous buds than ramets with all their chasmogamous flowers fertilized. These empirical data indicate that the fertility of chasmogamous flowers has a strong influence on cleistogamous flower production, and that the seasonal switching of chasmogamous and cleistogamous flower production in cleistogamous species can be explained by our model, which incorporates fluctuation in the fertility of chasmogamous flowers.

The effect of geitonogamous selfing

Our model suggests that the outcrossing advantage of chasmogamous flowers would be cancelled by the disadvantage of geitonogamous selfing that results in inbreeding depression. Since the viability of progeny produced by geitonogamous selfing of chasmogamous flowers is assumed to be equivalent to that of progeny from cleistogamous flowers, and since chasmogamous flower production requires a more reproductive allocation than cleistogamous flower production, chasmogamous flowers fertilized geitonogamously will have no advantage over cleistogamous flowers. The balance of an advantage of outcrossed and a disadvantage of geitonogamously selfed chasmogamous flowers would result in an ESS of simultaneous production of both types of flowers. In a previous theoretical study (Schoen and Lloyd, 1984), the reproductive allocation patterns predicted that chasmogamous reproduction is directly proportional to the resource; in contrast, cleistogamous reproduction was predicted to be constant and independent of the resource. Our model supports both the reproductive allocation pattern predicted by Schoen and Lloyd (1984) and its opposite pattern. In fact, the former – that is, higher dependency of chasmogamous flower production than cleistogamous flower production on available reproductive resources – has been observed in many cleistogamous species (Waller, 1980; Schmitt *et al.*, 1987; Ruiz de Clavijo and Jimenez, 1993). By contrast, in *Viola mirabilis*, cleistogamous flower production increases with plant size, whereas chasmogamous flower production is size-independent (Mattila and Salonen, 1995).

Although some studies have reported that inbreeding depression is not so important in selfing species (Stevens and Bougourd, 1988; Waller and Knight, 1989; Holtsford and Ellstrand, 1990), recent theoretical studies have shown that severe inbreeding depression can exist even in highly selfing populations due to the accumulation of moderate deleterious or recessive lethal mutations (Charlesworth *et al.*, 1990; Lande *et al.*, 1994). In addition, this prediction is supported by some empirical evidence (Yahara, 1992; Willis, 1993; Wolfe, 1993; Johnston and Schoen, 1995, 1996). In facultative cleistogamous plants, although total selfing (i.e. production of cleistogamous flowers and geitonogamy of chasmogamous flowers) tends to be high, sufficient inbreeding depression may exist. Thus, when inbreeding depression is rather severe and some extent of geitonogamous flowering occurs, the mixed strategies producing both chasmogamous and cleistogamous flowers can be an ESS. Therefore, the estimation of inbreeding depression and geitonogamous selfing rate in cleistogamous species is important when verifying an ESS model.

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