Why be completely outcrossing? Evolutionarily stable outcrossing strategies in an environment where outcross-pollen availability is unpredictable

Why be completely outcrossing? Evolutionarily stable outcrossing strategies in an environment where outcross-pollen availability is unpredictable

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ABSTRACT

We have developed a game theoretic model to analyse the conditions which favour complete outcrossing in environments where outcross-pollen availability is unpredictable, assuming that reproductive assurance when outcrossing is incomplete is possible. We assumed that a plant produces ovules before the availability of outcross-pollen for that year is known. We also assumed that there is a size–number trade-off of seeds, and the plant is not allowed to allocate its resources differently to its outcrossed and selfed seeds. These assumptions result in the reduction of the size of outcrossed seeds if the plant accepts selfed seeds as well. We found that complete outcrossing is likely to evolve if the degree of inbreeding depression is large, if the optimal seed size which maximizes the reproductive success (seed number × establishment probability of individual seeds) when there is no outcross-pollen limitation and no constraint on seed size is large, if the mean number of ovules potentially fertilized with outcross-pollen is large, or if the number of ovules potentially fertilized with outcross-pollen is not extremely variable. Thus, the best-of-both-worlds mechanism (maximizing both outcrossing and seed set with reproductive assurance by selfing) is not always advantageous even if outcross-pollen availability is unpredictable.

Keywords: best-of-both-worlds, delayed selfing, environmental variability, pollen availability, prepotency, reproductive assurance, selective abortion, self-incompatibility, selfing rate, size–number trade-off of seeds.

INTRODUCTION

Hermaphroditic plants show various rates of outcrossing, and the complete outcrosser, the intermediate selfer and the complete selfer are commonly observed in these plants (e.g. Aide, 1985; Waller, 1986). However, many theoretical studies have predicted a dichotomous outcome of evolution, resulting in either complete outcrossing or complete selfing, but not intermediate selfing (Lloyd, 1979, 1992; Lande and Schemske, 1985; Charlesworth *et al.*, 1990). Hence recent studies have focused on the factors which favour intermediate selfing, including sexual asymmetry (Charlesworth and Charlesworth, 1978; Gregorius, 1982), the

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resource costs of producing pollen-capture mechanisms (Iwasa, 1990; Sakai, 1995a), the decreasing total seed production associated with an increasing selfing rate (Lloyd, 1979), the disadvantage of selfed seeds in dispersal (Holsinger, 1986), over-dominance (Cambell, 1986; Holsinger, 1988; Charlesworth and Charlesworth, 1990; Uyenoyama and Waller, 1991), competition of self- and outcross-pollen on stigmas (Holsinger, 1991) and biparental inbreeding (Uyenoyama, 1986; Yahara, 1992).

On the other hand, selfing provides the advantage of reproductive assurance when outcrossing is incomplete (e.g. Schoen and Brown, 1991; Becerra and Lloyd, 1992; Lloyd, 1992; Cruzan and Barrett, 1993; Jones, 1994). This reproductive assurance is observed in plants with delayed selfing, in which selfing occurs as a result of stamen or style movements after the opportunity for outcrossing has passed, or in plants with prepotency, in which self-pollen is likely to fertilize ovules when there is less competition with outcross-pollen (reviewed by Lloyd and Schoen, 1992). Similarly, Becerra and Lloyd (1992) have reported that the success of selfed fruits in *Phormium tenax* is determined by the degree of competition with outcrossed fruits. Thus, these plants can maximize both outcrossing and seed set by selfing ovules which fail in outcrossing (i.e. the 'best-of-both-worlds'; Becerra and Lloyd, 1992). Several theoretical studies have also shown that the best-of-both-worlds mechanism is always advantageous in environments where outcross-pollen availability is at least partially unpredictable (Schoen and Brown, 1991; Lloyd, 1992).

However, plants with these systems could not prevent selfing completely even if outcrossing was complete. In fact, although outcross-pollen tubes grow more rapidly than self-pollen tubes, there are considerable variations in growth rate in both outcross- and self-pollen tubes (Hessing, 1989; Weller and Ornduff, 1989; Aizen *et al.*, 1990). Thus, after simultaneous application of outcross- and self-pollen in *Erythronium grandiflorum*, several fruits developed high proportions of selfed seeds, although most fruits developed high proportions of outcrossed seeds (Rigney *et al.*, 1993). Rigney (1995) has also reported that outcrossed ovules aborted in this species, although their probability of abortion was lower than that of selfed ovules. Similarly, in *Monarda fistulosa*, stigmas became receptive to cross-pollen before self-pollen, but the success rate of self-pollen in pollination was half that of outcross-pollen even in young flowers (Cruden *et al.*, 1984). Delayed selfing may also occur obligately even if the intensity of outcrossing is greater than a certain threshold. For example, delayed selfing is caused by corolla abscission in *Mimulus guttatus* (Dole, 1990) and this mechanism may result in selfing of some non-outcrossed ovules irrespective of the intensity of outcrossing. Moreover, in *Campsis radicans*, selfed seeds were able to develop in fruits with low selfing rates, although fruits with high selfing rates were likely to be aborted (Bertin and Sullivan, 1988).

Is the best-of-both-worlds mechanism always advantageous in environments where outcross-pollen availability is at least partially unpredictable? In this paper, we ask 'why be completely outcrossing' rather than 'why be an intermediate selfer', and develop a model for the evolutionarily stable outcrossing strategies in hermaphroditic plants, in which a size–number trade-off of seeds is assumed. In this model, we assume that a plant decides allocation to the female and male functions before the outcross-pollen availability of the year is known. The plant does not have the option to save some ovules for following years, even if only a limited amount of outcross-pollen is available. Also, the plant is unable to allocate its resources differently to its outcrossed and selfed seeds. These assumptions result in the reduction of the size of outcrossed seeds if the plant accepts selfed seeds as well. Using this model, we show that the best-of-both-worlds mechanism is not always

advantageous even if outcross-pollen availability is unpredictable, if seed size is negatively dependent on seed number, and if plants with the above systems cannot prevent selfing entirely when outcrossing is complete.

MODEL

The amount of outcross-pollen captured and self-pollen removed in this model is unpredictable (as in Sakai, 1996), in contrast to that in deterministic models (e.g. Sakai, 1993, 1995a,b; Sakai and Sakai, 1995). The complete outcrosser produces outcrossed seeds exclusively by preventing selfing, by some mechanism such as complete self-incompatibility. It may produce a small number of large seeds when outcrossing is incomplete, or a large number of small seeds when outcrossing is complete, as observed for many plants (e.g. Stanton *et al.*, 1987; Sakai and Sakai, 1995). Here, seed size is independent of seed number or positively related with it in some species (e.g. Michaels *et al.*, 1988). However, it should be noted that negative relationships between seed size and seed number might be masked by a third variable, such as plant resource status (Maddox and Antonovics, 1983; Michaels *et al.*, 1988; Venable, 1992; Sakai *et al.*, 1997). Thus, the above assumption cannot be applied only if size–number relationships are actually neutral or positive. On the other hand, the intermediate selfer produces selfed seeds, in addition to outcrossed seeds, when outcrossing is incomplete, by some mechanism such as delayed selfing or prepotency. We also assume a complete selfer: it produces selfed seeds exclusively without outcrossing. The present model is for animal-pollinated plants but the basic results are applicable to wind-pollinated plants.

A plant allocates T_f resources for ovule and pollen production in the flower stage:

$$T_f = c_f F + c_m M \tag{1}$$

where F and M are the numbers of ovules and pollen grains produced, and c_f and c_m are the cost of producing one ovule and one pollen grain (the cost includes production of other flower organs such as the accessories), respectively. In the fruit stage, T_s resources are newly available and are allocated to seed production. The seed size, S, is $T_s/(\text{seed number} + c)$, where the seed number of a plant may be variable and c is a constant ($c \geq 0$). The constant c is a constraint factor on seed size; seed size is constrained to vary within the range $S < T_s/c$ and it is not allowed to become unlikely large even if seed number is very small. This may be the result of some developmental and/or space constraints that prevent the plant from producing very large seeds. We assume that the intermediate selfer does not allocate its resources differently to its outcrossed and selfed seeds. This assumption is realistic because, for example, Becerra and Lloyd (1992) and Winn (1991) have reported that both outcrossed and selfed flowers on the same plants produce the same size of seeds. However, selfed seeds are smaller than outcrossed seeds in the same fruits in *Aquilegia caerulea* (Montalvo, 1992). This assumption may be an over-simplification for plants that can allocate resources differently to outcrossed and selfed seeds.

We next assume that larger seeds are able to develop more successfully to the next generation. Let $G(S)$ be the probability of seedling establishment from an outcrossed seed. As in Smith and Fretwell (1974), G is a sigmoid function of S and satisfies $G(0) = 0$. For selfed seeds, the probability of establishment is $(1 - \delta)G(S)$, where δ is the degree of inbreeding depression. We may assume the following function for numerical examples:

$$G(S) = \exp(-a/S) \tag{2}$$
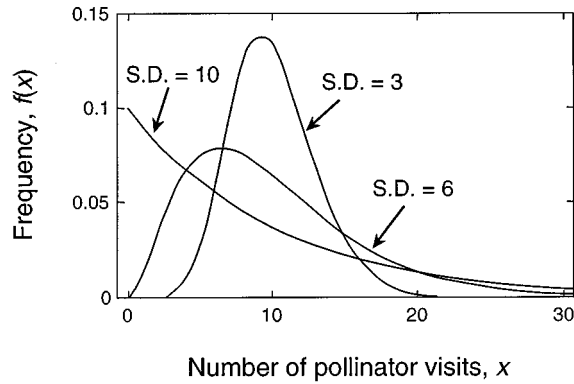
Fig. 1. Three examples of gamma distribution functions for the frequency distribution of the number of pollinator visits. The mean, m, is 10 in all functions and the standard deviation (s.d.) is $\sqrt{m/b}$.

The positive constant a is the 'optimal' seed size in the model of Smith and Fretwell (1974), which maximizes the reproductive success (the probability of seedling establishment × seed number) when there is no outcross-pollen limitation and no constraint on seed size ($c = 0$).

Let $f(x)$ be the probability that pollinators visit a plant x times during the flower stage, and e_f and e_m be the numbers of ovules fertilized and pollen grains removed per pollinator visit, respectively. Thus, all F ovules will develop to outcrossed seeds if $e_f x \geq F$, whereas $e_f x$ ovules will develop to outcrossed seeds if $e_f x < F$. Similarly, all M pollen grains will be removed if $e_m x \geq M$, whereas $e_m x$ grains will be removed if $e_m x < M$. We assume a gamma distribution function for f:

$$f(x) = \frac{b^{bm} x^{bm-1} \exp(-bx)}{\Gamma(bm)} \quad (3)$$

where m and $\sqrt{m/b}$ are the mean and the standard deviation, respectively, and $\Gamma(bm)$ is a Euler's gamma function. This function is bell-shaped if the standard deviation is small, whereas it is L-shaped if it is large (Fig. 1). This change in shape appears to be realistic because the frequency distribution of the number of pollinator visits may become L-shaped as the standard deviation increases. Thus, the mean and the standard deviation for the number of ovules potentially fertilized with outcross-pollen are $e_f m$ and $e_f \sqrt{m/b}$; for the number of pollen grains potentially removed, they are $e_m m$ and $e_m \sqrt{m/b}$, respectively.

We now define the expected reproductive success of a plant, which consists of the reproductive success due to outcrossed seeds, selfed seeds and pollen involved in fertilization on other plants. The intermediate selfer produces outcrossed seeds exclusively if $e_f x \geq F$; $S = T_s/(F + c)$ and the reproductive success due to outcrossed seeds is $G[T_s/(F + c)]F/2$ in this case. However, it produces $r(F - e_f x)$ selfed seeds in addition to $e_f x$ outcrossed seeds if $e_f x < F$, where the positive constant r (≤ 1) is the fraction of non-outcrossed ovules which develop to selfed seeds. Hence, $S = T_s/[e_f x + r(F - e_f x) + c]$ and the reproductive success due to outcrossed seeds and selfed seeds is $G[T_s/[e_f x + r(F - e_f x) + c]][e_f x/2 + (1 - \delta)r(F - e_f x)]$ in this case. Thus, the expected reproductive success of the intermediate selfer due to outcrossed seeds and selfed seeds is:

$$\varphi_{\mathrm{if}} = \frac{1}{2}\, G\left(\frac{T_{\mathrm{s}}}{F+c}\right) F \int_{F/e_{\mathrm{f}}}^{\infty} f(x)\mathrm{d}x +$$

$$\int_{0}^{F/e_{\mathrm{f}}} G\left[\frac{T_{\mathrm{s}}}{e_{\mathrm{f}}x + r(F - e_{\mathrm{f}}x) + c}\right]\left[\frac{e_{\mathrm{f}}x}{2} + (1-\delta)r(F - e_{\mathrm{f}}x)\right] f(x)\mathrm{d}x \quad (4\mathrm{a})$$

The first and the second terms on the right-hand side represent, respectively, the reproductive success when all ovules successfully develop to outcrossed seeds ($e_{\mathrm{f}}x \geq F$) and when some fraction of ovules fail in outcrossing ($e_{\mathrm{f}}x < F$). In the complete outcrosser, $S = T_{\mathrm{s}}/F$ and the reproductive success due to outcrossed seeds is the same as that for the intermediate selfer if $e_{\mathrm{f}}x \geq F$. However, it does not produce selfed seeds even if $e_{\mathrm{f}}x < F$; $S = T_{\mathrm{s}}/(e_{\mathrm{f}}x + c)$ and the reproductive success is $G[T_{\mathrm{s}}/(e_{\mathrm{f}}x + c)]e_{\mathrm{f}}x/2$ in this case. Thus, the reproductive success of the complete outcrosser due to outcrossed seeds, φ_{of}, is given by the right-hand side of equation (4a) with $r = 0$. On the other hand, in the complete selfer, $S = T_{\mathrm{s}}/(F + c)$ irrespective of x because F selfed seeds are always produced. Its reproductive success through selfed seeds is

$$\varphi_{\mathrm{sf}} = (1 - \delta)G[T_{\mathrm{s}}/(F + c)]\, F \quad (4\mathrm{b})$$

The reproductive success through pollen is the same for the complete outcrosser, the intermediate selfer and the complete selfer. Namely, the expected number of pollen grains removed is:

$$M\int_{M/e_{\mathrm{m}}}^{\infty} f(x)\mathrm{d}x + \int_{0}^{M/e_{\mathrm{m}}} e_{\mathrm{m}}x f(x)\mathrm{d}x \quad (5\mathrm{a})$$

The first and second terms represent the cases when all pollen grains are removed ($e_{\mathrm{m}}x \geq M$) and when fractions of pollen grains remain in the plant ($e_{\mathrm{m}}x < M$), respectively. Now, let W_1 be the probability that one pollen grain successfully fertilizes an ovule of another plant, and W_2 be the mean probability of seedling establishment from an outcrossed seed of other plants. W_1 is assumed to be the ratio of the total number of outcrossed ovules in the plants in the population to the total number of pollen grains removed from the plants. If the effects of rare mutants can be neglected,

$$W_1 = \frac{F_{\mathrm{w}}\displaystyle\int_{F_{\mathrm{w}}/e_{\mathrm{f}}}^{\infty} f(x)\mathrm{d}x + \displaystyle\int_{0}^{F_{\mathrm{w}}/e_{\mathrm{f}}} e_{\mathrm{f}}x f(x)\mathrm{d}x}{M_{\mathrm{w}}\displaystyle\int_{M_{\mathrm{w}}/e_{\mathrm{m}}}^{\infty} f(x)\mathrm{d}x + \displaystyle\int_{0}^{M_{\mathrm{w}}/e_{\mathrm{m}}} e_{\mathrm{m}}x f(x)\mathrm{d}x} \quad (5\mathrm{b})$$

where F_{w} and M_{w} are the values of F and M for the wild type. On the other hand, the wild type also produces outcrossed seeds with size $T_{\mathrm{s}}/(F_{\mathrm{w}} + c)$ if $e_{\mathrm{f}}x \geq F_{\mathrm{w}}$, whereas it produces those with the size $T_{\mathrm{s}}/[e_{\mathrm{f}}x + r(F_{\mathrm{w}} - e_{\mathrm{f}}x) + c]$ if $e_{\mathrm{f}}x < F_{\mathrm{w}}$ ($r = 0$ if the wild type is the complete outcrosser). Thus

$$W_2 = G\left(\frac{T_{\mathrm{s}}}{F_{\mathrm{w}} + c}\right)\int_{F_{\mathrm{w}}/e_{\mathrm{f}}}^{\infty} f(x)\mathrm{d}x + \int_{0}^{F_{\mathrm{w}}/e_{\mathrm{f}}} G\left[\frac{T_{\mathrm{s}}}{e_{\mathrm{f}}x + r(F_{\mathrm{w}} - e_{\mathrm{f}}x) + c}\right] f(x)\mathrm{d}x \quad (5\mathrm{c})$$

if the wild type is the intermediate selfer, whereas W_2 is given by the right-hand side of

equation (5c) with $r = 0$ if the wild type is the complete outcrosser. The expected reproductive success due to pollen is the product of formula (5a), W_1 and W_2 divided by 2:

$$\varphi_{\mathrm{m}} = \frac{1}{2} \left[M \int_{M/e_{\mathrm{m}}}^{\infty} f(x)\mathrm{d}x + \int_{0}^{M/e_{\mathrm{m}}} e_{\mathrm{m}} x f(x)\mathrm{d}x \right] W_1 W_2 \tag{5d}$$

The total expected reproductive success of the complete outcrosser, φ_{co}, the intermediate selfer, φ_{is}, and the complete selfer, φ_{cs}, is the sum of the reproductive success due to outcrossed seeds and/or selfed seeds, and due to pollen:

$$\varphi_{\mathrm{co}} = \varphi_{\mathrm{of}} + \varphi_{\mathrm{m}} \tag{6a}$$

$$\varphi_{\mathrm{is}} = \varphi_{\mathrm{if}} + \varphi_{\mathrm{m}} \tag{6b}$$

$$\varphi_{\mathrm{cs}} = \varphi_{\mathrm{sf}} + \varphi_{\mathrm{m}} \tag{6c}$$

If complete outcrossing with $F = F^*$ and $M = M^*$ is the evolutionarily stable strategy (ESS), any mutants of the complete outcrosser with $(F, M) \neq (F^*, M^*)$, and those of the intermediate selfer and the complete selfer with any values for F and M, cannot invade into the populations consisting of the ESS complete outcrossers. Similarly, if intermediate selfing with $F = F^*$ and $M = M^*$ is the ESS, any mutants of the intermediate selfer with $(F, M) \neq (F^*, M^*)$, and those of the complete outcrosser and the complete selfer with any values for F and M, cannot invade into the populations consisting of the ESS intermediate selfers. We calculate those F^* and M^* numerically to examine whether complete outcrossing or intermediate selfing (or complete selfing) is the ESS.

We concentrate on the arithmetic mean of reproductive success, which is suitable for long-lived perennial plants in a stationary population (Cohen and Dukas, 1990). In addition, the arithmetic mean could be applicable to annual plants in a stationary population where the mean reproductive success of plants does not change over the years, but where there are variances in reproductive success among plants within single years.

RESULTS

Figures 2A–D show the regions where complete outcrossing, intermediate selfing and complete selfing are the ESS, and contour maps of the ESS numbers of ovules produced, F^*. In these examples, seed size ranges from 1.82 to 3.33 (1.8-fold) in the case of minimum variation ($\delta = 1$ and $a = 3.5$ in Fig. 2A, where complete outcrossing is the ESS), except for the region where complete selfing is the ESS (the variance in seed size is zero in the complete selfer), and 0.45 to 3.33 (7.4-fold) in the case of maximum variation (δ is nearly 0.5 and $a = 0.5$ in Fig. 2A, where intermediate selfing is the ESS). Such magnitudes appear likely, since, for example, seed size varies as much as 2.1-fold in *Aster acuminatus* (Pitelka *et al.*, 1983), 4.2-fold in *Desmodium paniculatum* (Wulff, 1986), 5.7-fold in *Lilium auratum* (S. Sakai and A. Sakai, unpublished) and 15.8-fold in *Lomatium grayi* (Thompson, 1984).

Figure 2A shows the dependence of the ESS on the degree of inbreeding depression, δ, and the 'optimal' seed size when there is no outcross-pollen limitation and no constraint on seed size, a. Intermediate selfing (or complete selfing where $\delta < 0.5$) is the ESS if δ is small. In this region, the contribution of a selfed seed to reproductive success is large due to
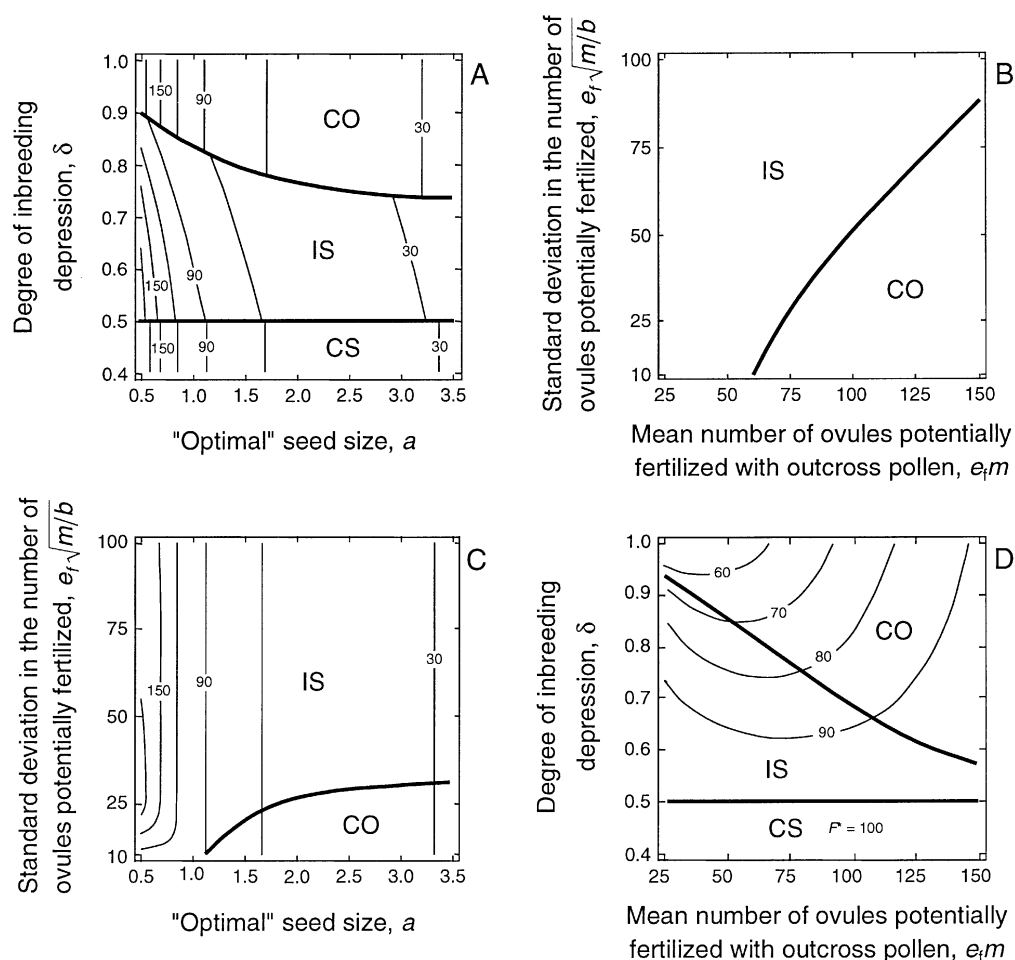
Fig. 2. The regions where complete outcrossing (CO), intermediate selfing (IS) and complete selfing (CS) are the evolutionarily stable strategies, and contour maps of the ESS numbers of ovules produced, F^*, depending on the degree of inbreeding depression, δ, the 'optimal' seed size that maximizes the reproductive success (seed number × establishment probability of individual seeds) when there is no outcross-pollen limitation and no constraint on seed size (i.e. the optimal seed size in the model of Smith and Fretwell, 1974), a, the mean number of ovules potentially fertilized with outcross-pollen, $e_f m$, and the standard deviation of the number of ovules potentially fertilized with outcross-pollen, $e_f \sqrt{m/b}$. The interval between contours is 30 in (A) and (C). $c = 30$, $c_f = 0.05$, $c_m = 0.0001$, $e_f = 5$, $e_m = 100$, $r = 1$, $T_f = 10$ and $T_s = 100$ in all figures. The other parameter values used are: $e_f m = 50$ and $e_f \sqrt{m/b} = 35$ in (A); $a = 1$ and $\delta = 0.7$ in (B); $\delta = 0.7$ and $e_f m = 50$ in (C); and $a = 1$ and $e_f \sqrt{m/b} = 50$ in (D).

the small δ and hence a plant should produce selfed seeds using non-fertilized ovules when outcrossing is incomplete. The ESS number of ovules produced, F^*, decreases with δ in this region. However, complete outcrossing is the ESS if δ is large and a plant does not produce selfed seeds even if non-fertilized ovules remain. In this region, the contribution of a selfed

seed to reproductive success is small, due to the large δ. Hence, it is advantageous to increase individual size of outcrossed seeds to enhance the probability of seedling establishment, rather than to increase seed number by selfing non-fertilized ovules. In other words, it is advantageous to produce a small number of large outcrossed seeds, rather than to produce a large number of small outcrossed and selfed seeds. Of course, even if δ is large, it is disadvantageous not to produce selfed seeds if the number of outcrossed seeds successfully produced happens to be very small. However, the advantage of complete outcrossing when outcrossing is moderate or complete makes up for this disadvantage. F^* is independent of δ where complete outcrossing or complete selfing is the ESS. On the other hand, in the region where δ is moderately high, intermediate selfing is the ESS if a is small, whereas complete outcrossing is the ESS if a is large. As a increases, the 'optimal' seed number when there is no outcross-pollen limitation and no constraint on seed size decreases and a plant decreases its number of ovules produced, F^*. The plant need not capture a large amount of outcross-pollen and hence complete outcrossing is rarely disadvantageous because most ovules will be fertilized with outcross-pollen even if the amount of outcross-pollen captured happens to be small. In other words, the increase in seed number by selfing non-fertilized ovules is small because few ovules remain, and hence the advantage of intermediate selfing becomes small as a increases even if δ remains constant. Complete outcrossing is thus the ESS even if δ is moderate.

Figure 2B shows the dependence of the ESS on the mean number of ovules potentially fertilized with outcross-pollen, $e_f m$, and the standard deviation of the number of ovules potentially fertilized with outcross-pollen, $e_f \sqrt{m/b}$. Intermediate selfing is the ESS if $e_f m$ is small or $e_f \sqrt{m/b}$ is large, whereas complete outcrossing is the ESS if $e_f m$ is large and $e_f \sqrt{m/b}$ is small. In the latter region, the amount of outcross-pollen captured is rarely small because $e_f m$ is large and $e_f \sqrt{m/b}$ is small; complete outcrossing is hence advantageous. F^* is almost constantly 100 in the entire region in this example.

Figure 2C shows the dependence of the ESS on a and $e_f \sqrt{m/b}$. Intermediate selfing is the ESS if a is small or $e_f \sqrt{m/b}$ is moderate or large, whereas complete outcrossing is the ESS if a is large and $e_f \sqrt{m/b}$ is very small, because the plant need not capture much outcross-pollen due to the large a, and the amount of outcross-pollen captured is rarely small because of the small $e_f \sqrt{m/b}$. F^* decreases with a as in Fig. 2A, and it is almost independent of $e_f \sqrt{m/b}$ as in Fig. 2B.

Figure 2D shows the dependence of the ESS on $e_f m$ and δ. Intermediate selfing is the ESS if $e_f m$ or δ is small (complete selfing is the ESS where $\delta < 0.5$), whereas complete outcrossing is the ESS if $e_f m$ and δ are large, because the plant can produce many vigorous outcrossed seeds. F^* increases with $e_f m$ and with decreasing δ in the region where complete outcrossing or intermediate selfing is the ESS, whereas F^* is constantly 100 in the region where complete selfing is the ESS.

DISCUSSION

The model presented here shows that the size–number trade-off of seeds is an important factor for the evolution of complete outcrossing in environments where outcross-pollen availability is unpredictable. Namely, it is advantageous to produce a small number of large outcrossed seeds rather than many small seeds, if the intensity of outcrossing is greater than a certain threshold. On the other hand, why does a plant not produce outcrossed seeds only if the intensity of outcrossing is greater than the threshold and produce both outcrossed

and selfed seeds if it is smaller than the threshold? This strategy is apparently optimal and complete outcrossing would never be the ESS if this strategy was possible. However, as stated in the Introduction, we suspect that plants are not capable of adopting this strategy. In addition, it may be advantageous to selectively abort damaged fruits (Stephenson, 1981) or fruits with small numbers of developing seeds (Lee and Bazzaz, 1982). Such selection can result in the development of selfed seeds in fruits with large numbers of seeds or in undamaged fruits. Thus, although we cannot say that no plant can adopt the above-mentioned strategy, we suggest that this strategy is impossible or disadvantageous for many plants due to other factors. In these plants, it can be advantageous to prevent selfing at the expense of reproductive assurance when the intensity of outcrossing is limited so as to enjoy complete outcrossing when intensity is great.

To test the present model, it is important to examine whether the best-of-both-worlds mechanism is not always advantageous, or whether producing outcrossed seeds exclusively while retaining non-outcrossed ovules could be advantageous when the intensity of outcrossing is greater than a certain threshold. Hand-pollination experiments may be useful to investigate this matter. For example, one could remove the anthers from all flowers of plants and bag the flowers to prevent natural outcrossing and selfing. Then, divide the plants in this group into several subgroups, hand-pollinate with outcross-pollen at different intensities from zero to excess for each subgroup. In a second group of plants, hand-pollinate with ample self-pollen after the same treatment. Then, if the above prediction is correct, the female reproductive success of a plant should be larger in subgroups of the first group than in the corresponding subgroups of the second group when the intensity of outcross hand-pollination is greater than a certain threshold, whereas it should be smaller in the former than in the latter if the intensity is less than that threshold.

Species or population comparisons may be useful to test the parameter effects shown in Fig. 2. However, in such comparisons, only qualitative tests should be performed, because many parameters may differ among species. Among the four independent parameters, the 'optimal' seed size, a, should be negatively correlated with the mean number of ovules potentially fertilized with outcross-pollen, $e_f m$. This is because large 'optimal' seed size tends to imply small 'optimal' seed number, and hence such plants need not capture a large amount of outcross-pollen. This means that plants can enjoy sufficient outcrossing even with the same value of $e_f m$, or a relatively large number of ovules can potentially be fertilized with outcross-pollen. Thus, the larger a is, the larger m is in relative terms.

Several other factors can favour complete outcrossing. First, structural constraints may prevent delayed selfing (Lloyd and Schoen, 1992; Lloyd, 1992). For example, in herkogamous or dichogamous species, delayed selfing can evolve only with reorganization of flower morphology or phenology, which may have other disadvantages (Lloyd, 1992). Second, perennial plants can reserve resources [or produce new ramets (Dole, 1992)] for the next year. This can enhance the evolution of complete outcrossing, but the size–number trade-off of seeds may still also be an important factor. This is because it is unlikely to be advantageous to produce a constant size of outcrossed seeds and to reserve all remaining resources for the next year irrespective of the intensity of outcrossing. The gain from reserved resources may diminish with the amount of reserved resources for the following reasons (Iwasa and Cohen, 1989): First, photosynthetic rate is usually a diminishing function of resource allocation to the vegetative parts and, for example, reserving double the amount of resources does not result in a doubling in the rate of photosynthates. Second,

there are risks of mortality and thus reserving resources may also be risky. Hence, it may be more advantageous to increase seed size or number using some additional resources rather than to reserve these resources for the following year. Thus, there still remains the problem of which is more advantageous, producing a small number of large outcrossed seeds or a large number of small outcrossed and selfed seeds.

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REFERENCES

Aide, T.M. 1985. The influence of wind and animal pollination on variation in outcrossing rates. *Evolution*, **40**: 434–435.

Aizen, M.A., Searcy, K.B. and Mulcahy, D.L. 1990. Among- and within-flower comparisons of pollen tube growth following self- and cross-pollinations in *Dianthus chinensis* (Caryophyllaceae). *Am. J. Bot.*, **77**: 671–676.

Becerra, J.X. and Lloyd, D.G. 1992. Competition-dependent abscission of self-pollinated flowers of *Phormium tenax* (Agavaceae): A second action of self-incompatibility at the whole flower level? *Evolution*, **46**: 458–469.

Bertin, R.I. and Sullivan, M. 1988. Pollen interference and cryptic self-fertility in *Campsis radicans*. *Am. J. Bot.*, **75**: 1140–1147.

Cambell, R.B. 1986. The interdependence of mating structure and inbreeding depression. *Theor. Pop. Biol.*, **30**: 232–244.

Charlesworth, D. and Charlesworth, B. 1978. Population genetics of partial male-sterility and the evolution of monoecy and dioecy. *Heredity*, **41**: 137–153.

Charlesworth, D. and Charlesworth, B. 1990. Inbreeding depression with heterozygote advantage and its effect on selection for modifiers changing the outcrossing rate. *Evolution*, **44**: 870–888.

Charlesworth, D., Morgan, M.T. and Charlesworth, B. 1990. Inbreeding depression, genetic load, and the evolution of outcrossing rates in a multilocus system with no linkage. *Evolution*, **44**: 1469–1489.

Cohen, D. and Dukas, R. 1990. The optimal number of female flowers and the fruits-to-flowers ratio in plants under pollination and resources limitation. *Am. Nat.*, **135**: 218–241.

Cruden, R.W., Hermanutz, L. and Shuttleworth, J. 1984. The pollination biology and breeding system of *Monarda fistulosa* (Labiatae). *Oecologia*, **64**: 104–110.

Cruzan, M.B. and Barrett, S.C.H. 1993. Contribution of cryptic incompatibility to the mating system of *Eichhornia paniculata* (Pontederiaceae). *Evolution*, **47**: 925–934.

Dole, J.A. 1990. Role of corolla abscission in delayed self-pollination of *Mimulus guttatus* (Scrophulariaceae). *Am. J. Bot.*, **77**: 1505–1507.

Dole, J.A. 1992. Reproductive assurance mechanisms in three taxa of the *Mimulus guttatus* complex (Scrophulariaceae). *Am. J. Bot.*, **79**: 650–659.

Gregorius, H.R. 1982. Selection in plant populations of effectively infinite size. II. Protectedness of a biallelic polymorphism. *J. Theor. Biol.*, **96**: 689–705.

Hessing, M.B. 1989. Differential pollen tube success in *Geranium caespitosum*. *Bot. Gaz.*, **150**: 404–410.

Holsinger, K.E. 1986. Dispersal and plant mating systems: The evolution of self-fertilization in subdivided populations. *Evolution*, **40**: 405–413.

Holsinger, K.E. 1988. Inbreeding depression doesn't matter: The genetic basis of mating-system evolution. *Evolution*, **42**: 1235–1244.

Holsinger, K.E. 1991. Mass-action models of plant mating systems: The evolutionary stability of mixed mating systems. *Am. Nat.*, **138**: 606–622.

Iwasa, Y. 1990. Evolution of the selfing rate and resource allocation models. *Pl. Sp. Biol.*, **5**: 19–30.

Iwasa, Y. and Cohen, D. 1989. Optimal growth schedule of a perennial plant. *Am. Nat.*, **133**: 480–505.

Jones, K.N. 1994. Nonrandom mating in *Clarkia gracilis* (Onagraceae): A case of cryptic self-incompatibility. *Am. J. Bot.*, **81**: 195–198.

Lande, R. and Schemske, D.W. 1985. The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution*, **39**: 24–40.

Lee, T.D. and Bazzaz, F.A. 1982. Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. *Ecology*, **63**: 1363–1373.

Lloyd, D.G. 1979. Some reproductive factors affecting the selection of self-fertilization in plants. *Am. Nat.*, **113**: 67–79.

Lloyd, D.G. 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *Int. J. Plant Sci.*, **153**: 370–380.

Lloyd, D.G. and Schoen, D.J. 1992. Self- and cross-fertilization in plants. I. Functional dimensions. *Int. J. Plant Sci.*, **153**: 358–369.

Maddox, G.D. and Antonovics, J. 1983. Experimental ecological genetics in *Plantago*: A structural equation approach to fitness components in *P. aristata* and *P. patagonica*. *Ecology*, **64**: 1092–1099.

Michaels, H.J., Benner, B., Hartgerink, A.P., Lee, T.D. and Rice, S. 1988. Seed size variation: Magnitude, distribution, and ecological correlates. *Evol. Ecol.*, **2**: 157–166.

Montalvo, A.M. 1992. Relative success of self and outcross pollen comparing mixed- and single-donor pollinations in *Aquilegia caerulea*. *Evolution*, **46**: 1181–1198.

Pitelka, L.F., Thayer, M.E. and Hansen, S.B. 1983. Variation in achene weight in *Aster acuminatus*. *Can. J. Bot.*, **61**: 1415–1420.

Rigney, L.P. 1995. Postfertilization causes of differential success of pollen donors in *Erythronium grandiflorum* (Liliaceae): Nonrandom ovule abortion. *Am. J. Bot.*, **82**: 578–584.

Rigney, L.P., Thomson, J.D., Cruzan, M.B. and Brunet, J. 1993. Differential success of pollen donors in a self-compatible lily. *Evolution*, **47**: 915–924.

Sakai, S. 1993. Allocation to attractive structures in animal-pollinated flowers. *Evolution*, **47**: 1711–1720.

Sakai, S. 1995a. Evolutionarily stable selfing rates of hermaphroditic plants in competing and delayed selfing modes with allocation to attractive structures. *Evolution*, **49**: 557–564.

Sakai, S. 1995b. A model for seed size variation among plants. *Evol. Ecol.*, **9**: 495–507.

Sakai, S. 1996. On ovule production in environments where pollinator or resource availability is unpredictable. *J. Theor. Biol.*, **183**: 317–327.

Sakai, S. and Sakai, A. 1995. Flower size-dependent variation in seed size: Theory and a test. *Am. Nat.*, **145**: 918–934.

Sakai, S., Sakai, A. and Ishii, H.S. 1997. Patterns of wing size variation in seeds of the lily *Cardiocrinum cordatum* (Liliaceae). *Am. J. Bot.*, **84**: 1275–1278.

Schoen, D.J. and Brown, A.H.D. 1991. Whole- and part-flower self-pollination in *Glycine clandestina* and *G. argyrea* and the evolution of autogamy. *Evolution*, **45**: 1651–1664.

Smith, C.C. and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.*, **108**: 499–506.

Stanton, M.L., Bereczky, J.K. and Hasbrouck, H.D. 1987. Pollination thoroughness and maternal yield regulation in wild radish, *Raphanus raphanistrum* (Brassicaceae). *Oecologia*, **74**: 68–76.

Stephenson, A.G. 1981. Flower and fruit abortion: Proximate causes and ultimate functions. *Ann. Rev. Ecol. Syst.*, **12**: 253–279.

Thompson, J.N. 1984. Variation among individual seed masses in *Lomatium grayi* (Umbelliferae) under controlled conditions: Magnitude and partitioning of the variance. *Ecology*, **65**: 626–631.

Uyenoyama, M.K. 1986. Inbreeding depression and the cost of meiosis: The evolution of selfing in populations practicing biparental inbreeding. *Evolution*, **40**: 388–404.

Uyenoyama, M.K. and Waller, D.M. 1991. Coevolution of self-fertilization and inbreeding depression II. Symmetric overdominance in viability. *Theor. Pop. Biol.*, **40**: 47–77.

Venable, D.L. 1992. Size–number trade-offs and the variation of seed size with plant resource status. *Am. Nat.*, **140**: 287–304.

Waller, D.M. 1986. Is there disruptive selection for self-fertilization? *Am. Nat.*, **128**: 421–426.

Weller, S.G. and Ornduff, R. 1989. Incompatibility in *Amsinckia grandiflora* (Boraginaceae): Distribution of callose plugs and pollen tubes following inter- and intramorph crosses. *Am. J. Bot.*, **76**: 277–282.

Winn, A.A. 1991. Proximate and ultimate sources of within-individual variation in seed mass in *Prunella vulgaris* (Lamiaceae). *Am. J. Bot.*, **78**: 838–844.

Wulff, R.D. 1986. Seed size variation in *Desmodium paniculatum*. I. Factors affecting seed size. *J. Ecol.*, **74**: 87–97.

Yahara, T. 1992. Graphical analysis of mating system evolution in plants. *Evolution*, **46**: 557–561.