

# Effects of Population Size and Metapopulation Dynamics on a Mating-System Polymorphism

John R. Pannell<sup>1</sup> and Spencer C. H. Barrett

Department of Botany, University of Toronto, 25 Willcocks Street, Toronto,  
Ontario M5S 3B2, Canada

E-mail: [john.pannell@plants.ox.ac.uk](mailto:john.pannell@plants.ox.ac.uk)

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The evolutionary dynamics of neutral alleles under the Wright–Fisher model are well understood. Similarly, the effect of population turnover on neutral genetic diversity in a metapopulation has attracted recent attention in theoretical studies. Here we present the results of computer simulations of a simple model that considers the effects of finite population size and metapopulation dynamics on a mating-system polymorphism involving selfing and outcrossing morphs. The details of the model are based on empirical data from dimorphic populations of the annual plant *Eichhornia paniculata*, but the results are also of relevance to species with density-dependent selfing rates in general. In our model, the prior selfing rate is determined by two alleles segregating at a single diploid locus. After prior selfing occurs, some remaining ovules are selfed through competing self-fertilisation in finite populations as a result of random mating among gametes. Fitness differences between the mating-system morphs were determined by inbreeding depression and pollen discounting in a context-dependent manner. Simulation results showed evidence of frequency dependence in the action of pollen discounting and inbreeding depression in finite populations. In particular, as a result of selfing in outcrossers through random mating among gametes, selfers experienced a “fixation bias” through drift, even when the mating-system locus was selectively neutral. In a metapopulation, high colony turnover generally favoured the fixation of the outcrossing morph, because inbreeding depression reduced opportunities for colony establishment by selfers through seed dispersal. Our results thus demonstrate that population size and metapopulation processes can lead to evolutionary dynamics involving pollen and seed dispersal that are not predicted for large populations with stable demography. © 2001 Academic Press

**Key Words:** selfing–outcrossing polymorphism; inbreeding depression; pollen discounting; metapopulation; extinction; colonisation; effective population size; fixation probability.

## INTRODUCTION

The expected outcome of drift versus selection in a population depends not only on its census size (the number of individuals counted) but also on its pattern of mating, its structure, and its dynamics (Crow and Kimura, 1970). Thus it is convenient to combine these various effects in an “effective” population size,  $N_e$ ,

which is really just a summary of the effect of several factors that jointly influence a population’s susceptibility to genetic drift.  $N_e$  is an important parameter that determines such processes as the rate of increase in homozygosity, the maintenance of genetic diversity, and the efficacy of selection acting on the population (Crow and Kimura, 1970; Hartl and Clark, 1997). It can in general be defined as the size of an ideal Wright–Fisher population that would experience the same effect of drift as the population under consideration.

<sup>1</sup> Current address: Department of Plant Sciences, South Parks Road, University of Oxford, Oxford, OX1 3RB, UK. Fax: +44(0) 1865 275074.

The Wright–Fisher model assumes that all individuals in a population during one generation are equally likely to be the parents of progeny in the next; this means that, in a population of constant size, each gene can expect to leave a single copy of itself in the following generation, with a variance of one (Crow and Kimura, 1970). Under the Wright–Fisher model, the parents of each progeny are assigned by drawing them from the population at random with replacement. This means that there is a  $1/N$  probability that the same parent is drawn twice; i.e., the Wright–Fisher model implies a selfing rate of  $1/N$ . However, many hermaphroditic animals and plants self-fertilise at rates that exceed this value; the effective size of such populations is given by

$$N_e = \frac{N}{1 + F},$$

where  $F = s/(2 - s)$  is the inbreeding coefficient and  $s$  is the probability that an individual is produced by selfing (Pollak, 1987; Nordborg, 2000). Thus one effect of self-fertilisation is to reduce the effective population size.

Other implications of selfing have also been the focus of much attention in the literature on plant mating-system evolution. For example, Fisher (1941) showed that a mutation causing an individual to self-fertilise would rapidly spread in a population in the absence of countervailing forces. One such force is the effect of inbreeding depression,  $\delta$  (Charlesworth and Charlesworth, 1987): if  $\delta < 0.5$ , a mutant increasing the selfing rate should spread, whereas outcrossing will be favoured if  $\delta > 0.5$  (Lande and Schemske, 1985; Charlesworth and Charlesworth, 1987). Another factor that will counter the automatic selection of selfing is pollen discounting, (i.e., a reduction in male siring success resulting from self-fertilisation; Nagylaki, 1976; Harder and Wilson, 1998). In particular, if pollen discounting is complete (i.e., if each pollen grain used in selfing were otherwise destined to sire a seed by outcrossing), a mutant increasing the selfing rate will be selectively neutral; similarly, in the absence of pollen discounting, such a mutant will be selectively neutral in a population in which  $\delta = 0.5$ . Even in such special cases, however, we might also expect inbreeding depression and pollen discounting to affect the effective size of a population. They may thus also affect the importance of drift and selection at linked loci, because both these factors alter the outcome of mating.

The effective population size will also be affected by the structure, or the degree of subdivision, of a species (Nagylaki, 1982; McCauley, 1991, 1995; Hedrick and Gilpin, 1997; Whitlock and Barton, 1997; Nagylaki,

1998; Pannell and Charlesworth, 1999, 2000). This is particularly the case when demes fluctuate in size or when a species has a metapopulation structure and is maintained under a balance of local extinctions and recolonisations (Slatkin, 1977; Whitlock and Barton, 1997; Pannell and Charlesworth, 1999). In such circumstances,  $N_e$  may be drastically reduced, with a concomitant reduction in times to fixation of alleles at neutral loci, as well as in the efficacy of selection at non-neutral loci that do not affect the migration or mating process (Barton and Whitlock, 1997). The evolutionary dynamics at loci that do interact with mating and colonisation, however, are likely to be more complicated. Mating-system genes typically interact with one another in a frequency-dependent manner (Fisher, 1930), so that the effect of selection upon them depends on more than just the population size relative to the strength of a constant selective advantage or disadvantage. Similarly, the process of population extinction and recolonisation may act selectively on mating-system genes (Baker, 1955; Lloyd, 1980; Pannell and Barrett, 1998) or on genes influencing dispersal (Olivieri *et al.*, 1997; Ronce and Olivieri, 1997), rather than simply amplifying the effects of drift.

In this paper, we examine the effects of population size and population turnover on several aspects of the evolutionary dynamics of a mating-system polymorphism, where predominant selfers and predominant outcrossers co-occur in a population. The particular mating process we have chosen to model is based on a known mating-system polymorphism in the tristylous, self-compatible, aquatic annual *Eichhornia paniculata* (Pontederiaceae) (Barrett, 1985), for which there is experimental evidence for context-dependent mating (Barrett *et al.*, 1989; Husband and Barrett, 1993). Mating-system dimorphisms of this type are known in several unrelated families of flowering plants, most commonly but not exclusively in heterostylous taxa (e.g., Ornduff, 1972; Ganders, 1975; Charlesworth and Charlesworth, 1979; Abbott and Woldendorp, 1985; Barrett *et al.*, 1989; Richards, 1997). The shift from outcrossing to selfing in *E. paniculata* has recently been cited as one of the few examples of the role of genetic drift in contributing towards an adaptive peak shift, as hypothesised in Wright's shifting balance theory (Coyne *et al.*, 1997).

We are particularly interested in the way in which the effects of inbreeding depression and pollen discounting interact with population size and extinction-recolonisation dynamics. We focus on this issue specifically in the context of different "modes" of selfing (Lloyd and Schoen, 1992), i.e., "competing selfing" as a result of random mating in a finite population, as assumed in the Wright–Fisher model, and "prior selfing," the rate of which is

determined by the mating-system genotype. Our results demonstrate that times to fixation and fixation probabilities of neutral and selected alleles are indeed affected by such interactions, and that the effects of population turnover on mating-system alleles depend in complex ways on the mating system and the colonisation and migration process. Our study uses simulations to explore the effect of these factors on probabilities of, and times to, fixation of alleles at the mating-system locus. Essentially, our results provide insights into the effects of the mating system and population dynamics on the inbreeding effective size of a species.

## THE MODEL

### Details of the Mating Process

We have adopted in our model the same genetic basis of control of the mating-system as is displayed by *E. paniculata* (Barrett *et al.*, 1989; Fenster and Barrett, 1994). In *E. paniculata*, a recessive allele modifies the outcrossing mid-styled morph, bringing an anther close to the stigma and causing the plant to self-fertilise. Our model captures this by assuming a single mating-system locus segregating for two alleles, *A* and *a*, with *A* fully dominant over *a*. Let *N* be the size of the population or neighbourhood within which mating occurs, and let  $g_1$ ,  $g_2$ , and  $g_3$  be the numbers of individuals in the population or neighbourhood of genotypes *AA*, *Aa*, and *aa*, respectively, such that  $N = g_1 + g_2 + g_3$ . All plants are cosexual, and mating-system phenotypes differ only in the proportion of their ovules that are selfed prior to any outcrossing that may occur (prior self-fertilisation; Lloyd, 1979). Thus genotypes *AA* and *Aa* self a fraction  $s_1$  and genotype *aa* a fraction  $s_2$  of their ovules prior to subsequent random fertilisation of the unselfed ovules in the population. Ovules in the remaining unselfed proportion,  $1 - s_i$  (where  $i = 1, 2$ ), are fertilised by pollen that has not been discounted during self-pollination. This second phase of mating occurs randomly by “mass-action” pollination (Holsinger, 1991; Harder and Wilson, 1998), with each ovule uniting with a given pollen haplotype according to its frequency in the combined pollen pool. This idealised depiction of mating corresponds to the Wright–Fisher model, modified by introducing selfing and pollen discounting.

In accordance with what is known about the genetics of the mating-system locus in *E. paniculata*, we assumed that the allele for the outcrossing morph is recessive to that of the selfer, although simulations with a dominant

allele for outcrossing produced very similar results. For the results presented here, we have assigned a “prior-selfing” rate,  $s$ , of 0.2 to the outcrosser and 0.8 to the selfer, in accordance with values from populations of *E. paniculata* (see, for example, Table 5 in Barrett *et al.*, 1989). Altering these values did not change our simulation results qualitatively as long as there was at least some difference in the selfing rate between the two mating-system phenotypes. This means that a proportion  $s$  of a plant’s ovules is selfed automatically, and that the fate of the balance depends on the context in which the plant finds itself.

Let  $D$  be the rate of pollen discounting resulting from self-fertilisation, such that the fraction  $Ds_i$  of a plant’s pollen is used up (or otherwise lost) through the process of prior self-fertilisation. We assume for convenience that each plant produces one unit of pollen, so that plants contribute  $1 - Ds_i$  pollen to the pollen pool. Hence the total amount of pollen in the pollen pool of each mating neighbourhood, after prior selfing, is

$$P = (1 - Ds_1)(g_1 + g_2) + (1 - Ds_2)g_3.$$

The fractions of the pollen pool composed of pollen haplotypes *A* and *a*, respectively, are

$$P_A = \frac{(1 - Ds_1)(g_1 + g_2/2)}{P}$$

and

$$P_a = \frac{(1 - Ds_1)g_2/2 + (1 - Ds_2)g_3}{P}.$$

In an infinite population, any ovule not selfed through prior self-fertilisation (i.e., the proportion  $1 - s_i$  of ovules produced by each plant) will be outcrossed. The reason for this is that, when  $N$  is large, each individual contributes a negligible fraction of pollen to the total pollen pool in the population, and so effectively all pollen reaching its unselfed ovules will be outcross pollen. However, in a mating neighbourhood in which  $N$  is small, this will no longer be true. With  $N$  small, each individual’s pollen may constitute a significant proportion of the pollen pool, and therefore a proportion of its ovules not selfed through prior self-fertilisation will be self-fertilised by its own pollen through random mating. This affects neither the expressions above for the contribution of each pollen haplotype to the pollen pool, nor the proportion of zygotes of each genotype formed. It does, however, become important for the transmission of

TABLE 1

List of Symbols and Variables Used in the Model with Their Definitions

Symbol	Definition
$g_1$	Number of individuals of genotype $AA$ (genotype 1)
$g_2$	Number of individuals of genotype $Aa$ (genotype 2)
$g_3$	Number of individuals of genotype $aa$ (genotype 3)
$g'_i$	Number of progeny produced of genotype $i$
$G$	Number of ovules produced per individual
$P$	Total pollen dispersed for outcrossing in the mating neighbourhood
$P_i$	Fraction of pollen dispersed in the neighbourhood that is haplotype $i$
$N$	Total number of individuals in the mating neighbourhood
$M$	Number of demes in the metapopulation
$K$	Carrying capacity of each site (population)
$s_i$	Selfing rate of phenotype $i$
$\delta$	Level of inbreeding depression
$D$	Rate of pollen discounting
$E$	Probability of colony extinction
$I$	Mean number of immigrants to a colony per generation

genes to subsequent generations when selfed zygotes suffer from inbreeding depression. We thus incorporate into the model the parameter  $\delta$ , the level of inbreeding depression suffered as a result of selfing; i.e., we assume that a proportion  $\delta$  of selfed zygotes are inviable. Finally, we assume that each individual produces  $G$  ovules and that pollen availability does not limit seed set (so that all ovules are ultimately fertilised). Parameters used in the model are listed in Table 1 for reference.

We can now calculate the numbers of progeny produced by genotypes  $AA$ ,  $Aa$ , and  $aa$  in any mating neighbourhood; let these be  $g'_1$ ,  $g'_2$ , and  $g'_3$ , respectively. As an illustration, we give here a breakdown of the recursion equation only for  $g'_3$  (equations for  $g'_1$  and  $g'_2$  are presented in the Appendix). For clarity, we leave expressions in their most explicit form so that the terms for ovule and pollen haplotypes to be multiplied are clearly seen. In the expression, parameters governing ovule production (as well as inbreeding depression that determines the fate of those ovules) precede those determining the appropriate pollen haplotype frequencies with which they are multiplied. Pollen parameters are written within curly brackets.

Note that  $aa$  progeny may be produced as a result of three different mating events. Some progeny may be produced by prior self-fertilisation, of which there will be

$$g'_{3(\text{prior})} = Gg_3s_2(1-\delta)\{1\} + G\frac{g_2}{2}s_1(1-\delta)\left\{\frac{1}{2}\right\}. \quad (1)$$

The first term accounts for selfed ovules produced by individuals of genotype  $aa$  and the second for selfed ovules of haplotype  $a$  produced by individuals of genotype  $Aa$  and fertilised by self-pollen of haplotype  $a$ . Progeny may also be produced by outcrossing after prior self-fertilisation has taken place:

$$g'_{3(\text{out})} = Gg_3(1-s_2)\left\{\frac{(1-Ds_2)(g_3-1) + (1-Ds_1)g_2/2}{P}\right\} + G\frac{g_2}{2}(1-s_1)\left\{\frac{(1-Ds_2)g_3 + (1-Ds_1)(g_2-1)/2}{P}\right\}. \quad (2)$$

The first term accounts for those progeny resulting from the union of haplotype  $a$  ovules produced by genotype  $aa$  individuals with  $a$  haplotype pollen in the pollen pool. The second term accounts for the union of haplotype  $a$  ovules produced by genotype  $Aa$  individuals (only a half of their ovules are of haplotype  $a$ ) with haplotype  $a$  pollen. The bracketed term on the right-hand side of each term is the proportion of haplotype  $a$  outcrossing pollen. Note that in the first term the number of genotype  $aa$  individuals contributing to the outcross pollen pool is  $g_3 - 1$ . Here  $g_3$  is reduced by one because we wish to ignore the contribution of self pollen to the pollen pool; ovules fertilised by this self pollen are accounted for in (3) below. Similarly,  $g_2$  is reduced by one in the second term.

Finally, progeny of genotype  $aa$  may be produced by individuals of genotypes  $Aa$  and  $aa$  through selfing when  $N$  is finite:

$$g'_{3(\text{comp})} = Gg_3(1-s_2)(1-\delta)\left\{\frac{(1-Ds_2)}{P}\right\} + G\frac{g_2}{2}(1-s_1)(1-\delta)\left\{\frac{(1-Ds_2)/2}{P}\right\}. \quad (3)$$

Total  $g'_3$  produced in the mating neighbourhood will equal  $g'_{3(\text{prior})} + g'_{3(\text{out})} + g'_{3(\text{comp})}$ . The recursion equations for  $g'_1$ ,  $g'_2$ , and  $g'_3$  (see the Appendix) were used to calculate genotype frequencies in population trajectories over time. In all simulations described below, the frequencies of alleles  $A$  and  $a$  were started at 0.5, with frequencies of genotypes at Hardy–Weinberg equilibrium. In a sense, this is an arbitrary starting frequency, but it has the advantage that, for a neutral locus, fixation probabilities of alternative alleles are expected to be equal, so that deviations from neutral expectation can be observed in the most straightforward manner.

Our model can be thought of in terms that relate directly to the familiar Wright–Fisher model, with the following modification. Each plant produces  $x \gg N$  ovules and  $y \gg N$  pollen grains, a total number  $y(1 - Ds)$  of which are contributed to the “outcross” pollen pool. The ovules have two possible fates:  $x(1 - \delta)s$  of them are produced by prior selfing, and  $x(1 - s)$  are contributed to a pool of ovules that are fertilised randomly by pollen from the outcross pollen pool. In a population composed of only one mating-system phenotype,  $x(1 - s)(1 - 1/N)$  of these ovules will be outcrossed, while  $x(1 - s)/N$  of them will produce zygotes as a result of competing selfing. Of these selfed zygotes, only  $x(1 - s)(1 - \delta)/N$  survive. At the end of the mating process in a monomorphic population, there will therefore be a total of  $Nx(1 - \delta)s + x(1 - s)(1 - \delta)$  selfed and a total of  $Nx(1 - s)(1 - 1/N)$  outcrossed zygotes. The population size for the next generation is regulated by choosing  $N$  progeny at random from the combined pool of outcrossed and viable selfed progeny. Note that with  $s = \delta = 0$ , this mating scheme reduces to the Wright–Fisher model. Note also that the same basic scheme applies for the dimorphic populations of our model, except that each of the morphs contribute different quantities of pollen and ovules to the selfing and outcrossing pools.

### Finite Population Model

The evolution of an individual population was simulated 10,000 times for several values of  $\delta$  and  $D$  and for population sizes,  $N$ , ranging from 1 to 512. Seed recruitment into the next generation was simulated by randomly sampling  $N$  individuals from the distribution of genotypes given by the recursion equations above; i.e., the probability of sampling an individual of a particular genotype is simply the frequency of that genotype in the seed pool, so that the numbers of the three genotypes sampled for the following generation followed a trinomial distribution. Biologically this means that while large numbers of seeds are produced by individuals each generation ( $G$  is large), on average only one of these establishes as a mature plant (i.e., the population, and each neighbourhood, is at carrying capacity).

### Metapopulation Model

We simulated the maintenance of a selfing–outcrossing polymorphism in a metapopulation consisting of  $M$  identical sites that may be occupied by colonies (or populations) of individuals of the three genotypes described above. Each colony comprised a single mating

neighbourhood. At the beginning of each generation, each existing colony could go extinct with a constant probability  $E$ . Surviving colonies then reproduced according to the same recursion equations described above, and seed dispersal occurred at the end of each generation. Each site could support a maximum of  $K$  individuals. Colonies that exceeded this value after reproduction were truncated back to  $K$  so that genotype frequencies remained unaltered.  $K$  was assumed to be large enough for any stochastic effects of truncation to be ignored. These growth dynamics simulated the competitive effects of crowding on colony size and reproductive output.

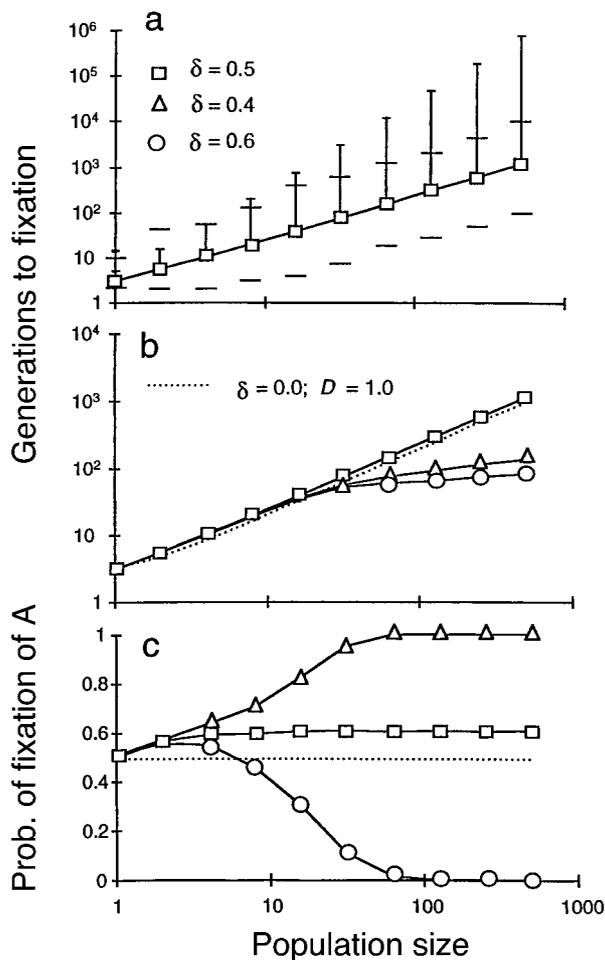
Gene flow between colonies was assumed to occur solely through seed dispersal. The mean number of seeds immigrating into each site each generation,  $I$ , was held constant for the duration of each simulation, with a Poisson number of immigrants or colonists arriving at each deme. Although  $I$  might more realistically depend on the density and size of occupied sites in the metapopulation, holding its value fixed allowed us to observe directly the effect of specific changes in  $I$  on the maintenance of the polymorphism. The simulations examined the dynamics of an “island model” of dispersal, where all colonies in the metapopulation contributed to the migrant pool according only to their size and composition, and independent of the spatial arrangement of sites. The probability of fixation of the dominant allele  $A$  for increased selfing was estimated on the basis of 1000 simulations of a metapopulation with  $M = 20$  sites for each of three values each of  $I$  and  $E$ .

## RESULTS AND DISCUSSION

### Finite Populations

In a finite population in which  $\delta = 0.5$  and  $D = 0$ , the mean time to fixation of either allele was proportional to the population size, with  $\bar{T} = 2.26N$  (Fig. 1a). This proportionality confirms the neutrality of the mating-system locus under these parameter values (Crow and Kimura, 1970) and provides a useful check for the simulations. Kimura (1955; see Hard and Clark, 1997) showed that a neutral allele should drift to fixation from an initial frequency of 0.5 (as here) within a mean of  $2.8N_e$  generations (where  $N_e$  is the effective population size). Thus the pattern of inbreeding in our model reduced  $N_e$  to a fraction 0.81 the size of a Wright–Fisher population with the same total population size.

When neutrality at the mating-system locus was achieved as a result of pollen discounting (i.e.,  $\delta = 0$  and



**FIG. 1.** The mean number of generations to fixation of either allele,  $\bar{T}$  (a and b), and the probability of fixation of dominant allele  $A$  (c) as a function of the population (mating neighbourhood) size,  $N$ . (a) Only one level of inbreeding depression is shown,  $\delta = 0.5$ ; pollen discounting,  $D$ , was 0.0 in all curves except the dotted curve in graphs b and c. (For  $\delta = 0.5$ , the mating system locus is effectively neutral.)  $\bar{T}$  is shown together with the variance in  $T$  (positive error bars) and the minimum and maximum  $T$  (the longer horizontal bars) recorded in 10,000 simulations for each population size.  $\bar{T} = (2.262 \pm 0.004) * N$  (estimate  $\pm$  se;  $P < 0.0001$ ); intercept does not differ from zero ( $P = 0.845$ ). (b)  $\bar{T}$  is plotted for  $\delta = 0.5, 0.4$ , and  $0.6$  (all with  $D = 0.0$ ) and for  $D = 1.0$  (with  $\delta = 0.0$ ). For  $N > 1$ ,  $\bar{T}$  ( $\delta = 0.5, D = 0.0$ ) =  $(1.172 \pm 0.006) * \bar{T}$  ( $\delta = 0.0, D = 1.0$ ) (mean  $\pm$  se). (c) The probability that dominant allele  $A$  for greater selfing is eventually fixed in a population of size  $N$ . Symbols are as in (a) and (b).

$D = 1$ ),  $\bar{T}$  increased linearly with  $N$  as before, but for  $N > 1$ ,  $\bar{T}$  was about 1.17 times lower than when inbreeding depression countered automatic selection for selfing (dotted line in Fig. 1b). Thus, although inbreeding depression and pollen discounting can both counter the automatic selective advantage of an allele for greater selfing, a further effect of pollen discounting is to reduce the effective population size in a way that inbreeding depression does not.

These effects are likely due to the fact that inbreeding depression causes a reduction in the proportion of inbred progeny in the population (a proportion  $\delta$  of the inbred progeny do not reproduce), whereas pollen discounting reduces the number of outcrossed progeny sired by selfers. The rate of increase in homozygosity in the population is thus higher under the action of pollen discounting than under that of inbreeding depression.

As expected, in the absence of pollen discounting, deviations in  $\delta$  from 0.5 caused selection to act at the mating-system locus in favour of either greater selfing ( $\delta < 0.5$ ) or greater outcrossing ( $\delta > 0.5$ ) in such a way as to decrease the time to fixation (Fig. 1b) and to alter the probability of fixation from 0.5 (uppermost and lowermost curves in Fig. 1c). This dominance of selection over drift as indicated by deviations from proportionality between  $\bar{T}$  and  $N$  was evident when  $N$  was greater than about 20; for smaller population sizes, drift predominated, and  $\bar{T}$  was proportional to  $N$ . A similar effect on the relation between  $\bar{T}$  and  $N$  was also observed for  $D > 0$  when  $\delta$  deviated from the value required for neutrality (results not shown). However, the dominance of selection over drift on fixation probabilities was evident for much smaller population sizes (Fig. 1c; note the deviations from 0.5 occurred for  $N > 1$ ).

Figure 1c illustrates a somewhat surprising result of our simulations. We should expect the probability of fixation of alleles at a neutral locus to be equal to their frequency in the population, independent of the population size (Wright, 1931). In our simulations, in which initial allele frequencies were always 0.5, we thus expected an equal probability of fixation for both alleles. This is what we found for the parameter combination  $D = 1$  and  $\delta = 0$  (dotted line in Fig. 1c). However, in simulations with  $D = 0$  and  $\delta = 0.5$ , the probability of fixation of the allele for greater selfing settled at about 0.6 for  $N$  greater than a few individuals (square symbols in Fig. 1c). Thus inbreeding depression, and not pollen discounting, caused a “fixation bias” at the mating-system locus, such that the allele for greater selfing was fixed more often than expected under neutrality. This fixation bias is not a straightforward effect of selection. As the curves for  $\delta = 0.4$  and  $\delta = 0.6$  illustrate, we expect the fixation probability of the selected allele to increase with increasing population size, but the fixation bias observed for cases where the automatic selection of selfing was neutralised by inbreeding depression (such as when  $D = 0$  and  $\delta = 0.5$ ; Fig. 1c) was independent of population size.

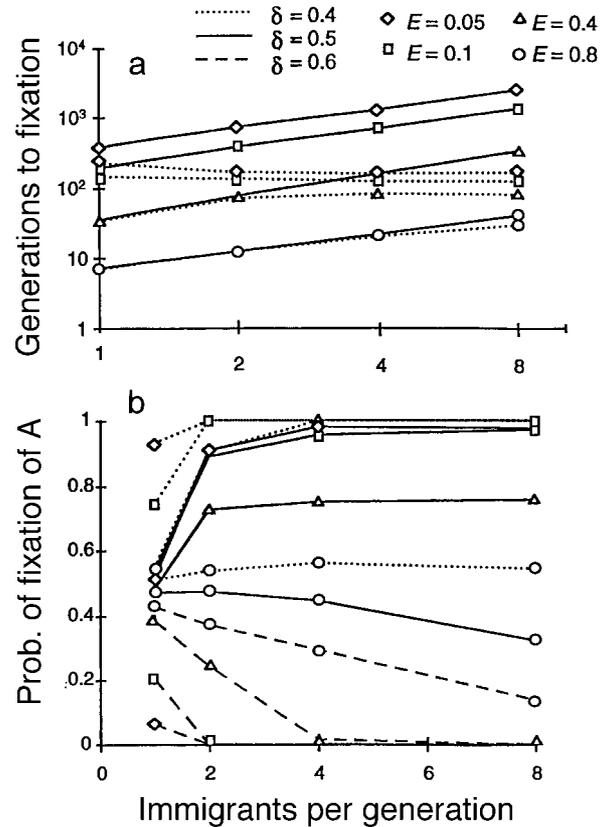
The fixation bias of an allele for greater selfing appears to be a result of the second phase of self-pollination, which occurred during random mating among gametes in finite populations. Recall that in our model there were

two modes of selfing. First, some ovules were selfed by “prior self-fertilisation” following the plant’s genetically determined propensity to self-fertilise a given fraction of its ovules. And second, the remaining ovules were fertilised competitively by pollen sampled randomly from the population pollen pool (following the Wright–Fisher scheme), and some of these will have been fertilised by self pollen. Because outcrossers had more ovules still available for fertilisation than selfers, more of their progeny will have been selfed competitively in this way, and hence more will have been lost through the effects of inbreeding depression. This explanation was verified by simulating a modified model in which inbreeding depression affected only prior-selfed ovules. In these simulations (results not shown), the fixation bias of selfing disappeared, and the probability of fixation of both alleles was always 0.5.

The biased fixation of alleles for greater prior selfing is an outcome of selection against competing selfing, and as such is analogous to Lloyd’s (1992) prediction that geitonogamous selfing is always disadvantageous when it occurs. In Lloyd’s model, geitonogamy was more severe when  $N$  was small. This might appear to contrast with the outcome of our model, in which the observed fixation bias was independent of the population size when  $N$  was greater than a few individuals (see Fig. 1c). However, the difference can be explained by noting that increasing  $N$  has two effects: not only does it reduce the rate of competing selfing and therefore the intensity of selection, but it also reduces the effect of drift, thereby increasing the time to fixation over which selection can act. It is remarkable that decreasing the proportion of ovules lost to inbreeding depression through competing selfing in larger populations was exactly counterbalanced by increasing the number of generations over which this diminished effect was manifest.

### Metapopulations

With  $\delta = 0$  and  $D = 1$ , both alleles segregating at the mating-system locus in a metapopulation were always equally likely to be fixed in a metapopulation (results not shown). However, simulation results concerning fixation probabilities and times to fixation were more complicated for a metapopulation in which inbreeding depression was acting, and they depended both quantitatively and in direction on the extinction rate,  $E$ , and on the number of colonists,  $I$  (Fig. 2). We will therefore focus our attention here exclusively on results of simulations in which  $\delta = 0.5$  and  $D = 0$ . In interpreting these results, it is instructive to compare Figs. 2a and 2b (simulations with population turnover) with Figs. 1b and 1c (simulations of a finite population), respectively.



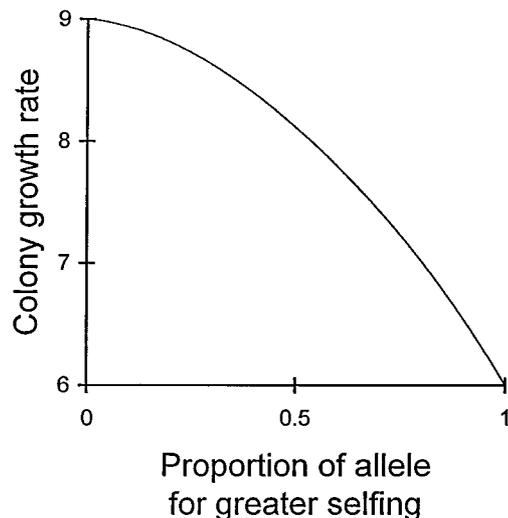
**FIG. 2.** (a) The mean number of generations to fixation of either mating-system allele (calculated over 1000 simulations for each parameter combination), plotted against the actual number of immigrants to each site per generation. Curves are shown for four values of  $E$  and two values of  $\delta$  (the outcomes for  $\delta = 0.6$  were similar to those for  $\delta = 0.4$  and are not shown). For all curves,  $D = 0$ . (b) The probability of fixation of dominant allele  $A$  for greater selfing in a metapopulation with 20 populations, plotted against the actual number of immigrants arriving at each site per generation (according to an island model of dispersal); see text for description of simulation conditions. Simulation outcomes are shown for three levels of inbreeding depression,  $\delta$ , and four extinction rates,  $E$ . In all cases,  $K = 1000$ ,  $G = 10$ .

In a metapopulation with population turnover, the average time to fixation of the allele for predominant selfing,  $\bar{T}$ , increased linearly with  $I$  at a rate that depended on  $E$  ( $\delta = 0.5$  and  $D = 0$ ; unbroken lines in Fig. 2a). In particular, for the parameter combinations assumed for the curves in Fig. 2a, a regression of the natural logarithm of  $\bar{T}/I$  (calculated for each of the four unbroken curves in the figure) against  $E$  was linear ( $r^2 = 0.994$ ;  $P = 0.0029$ ;  $df = 3$ ), such that  $\bar{T} = I \times \exp(5.81 - 5.36E)$ . Reducing the number of colonists or increasing the frequency of population turnover thus caused a linear reduction in the inbreeding effective size of the metapopulation. This reduction of  $N_e$  as a result of extinction and colonisation is well understood for simpler models of mating in a

metapopulation with similar structure and dynamics (e.g., Hedrick and Gilpin, 1997; Whitlock and Barton, 1997; Pannell and Charlesworth, 1999). It is due to the great increase the variance in reproductive success amongst individuals as a result of the rapid growth following colonisation (Pannell and Charlesworth, 2000). For a neutral locus in such a metapopulation, this implies that the time to fixation will be reduced both by increases in the extinction rate and by reductions in the size of the bottleneck that occurs during colonisation. Our simulations behaved accordingly. The linear increase in time to fixation with increases in the mean number of immigrants follows from the fact that the effective size of a population is determined much more by the size of bottlenecks through which it passes than by the maximum size it may ultimately reach (Crow and Kimura, 1970).

When the mating-system locus was not selectively neutral, i.e., with  $\delta = 0.4$  or  $0.6$  and  $D = 0$ ,  $\bar{T}$  was reduced below neutral expectation, especially with increasing  $I$  (e.g.,  $\delta = 0.4$  in Fig. 2a). This balance between selection and drift at the mating-system locus is further illustrated in Fig. 2b. With  $D = 0$  and  $\delta \neq 0.5$  (e.g.,  $\delta = 0.4$  or  $0.6$ ; dotted and broken lines in Fig. 2b), increases in  $E$  and reductions in  $I$  both caused selection to be less effective in driving the advantageous allele to fixation due to the increased importance of drift (i.e., the fixation bias to one or other allele was reduced). This parallels the effect of reductions in  $N$  on the fixation probability at the mating-system locus, depicted in Fig. 1c. With  $\delta = 0.5$  (non-selected behaviour), we observe a similar but more extreme manifestation of the fixation bias of the allele for greater selfing as seen in a finite population without extinction (compare Figs. 1c and 2b). The effect is complicated, however, because very high extinction rates actually reversed the fixation bias toward the allele for greater outcrossing.

This tendency for outcrossers to be fixed more frequently at high  $E$  can be explained by selective processes at the metapopulation level. Because the progeny of outcrossers were less likely to suffer from the effects of inbreeding depression in established populations than those of selfers, predominant outcrossers produced and dispersed relatively more seeds. This is illustrated for our model in Fig. 3, in which colony growth rates (i.e., seed productivities) are plotted against the frequency of the allele for greater selfing in the population. Populations with a high frequency of the allele for greater selfing (i.e., with a high mean selfing rate) produced fewer seeds (and experienced a smaller growth rate) than those with low selfing rates. Such populations contributed a smaller proportion of the seeds being dispersed between sites, and hence individuals



**FIG. 3.** The growth rate of colonies starting with different frequencies of alleles for greater selfing and outcrossing. Colonies with a higher frequency of the allele for greater outcrossing grew more quickly than those for greater selfing. For these simulations,  $D = 0$ ,  $\delta = 0.5$ , and  $G = 10$ .

comprising them were selected against at the metapopulation level. This is similar to the assumption made in Holsinger's (1986) model of the evolution of self-fertilisation in a structured population. In that model, it was assumed that selfers produced poorer quality colonisers than did outcrossers, whereas here the effects of inbreeding depression ensured that selfers dispersed fewer seeds to other sites.

The higher fixation probability of outcrossers relative to selfers in our metapopulation simulations was thus apparently due to the greater seed productivity of outcrossers. Other studies have emphasised the role of reproductive assurance in selecting for selfing in colonising species (i.e., Baker's Law; Baker, 1955, 1967; Lloyd, 1980; Pannell and Barrett, 1998). It is important to note that we did not consider differences in reproductive assurance *per se*; as both predominant selfers and predominant outcrossers could found colonies as solitary individuals (since they were assumed to be self-compatible), they were thus always assured of some reproductive success. In an important sense, it is the predominant outcrossers in our model that possessed properties ideally suited to the colonising habit, not the selfers. Both selfers and outcrossers were assured of reproductive success through selfing during colonisation, but once colonies became established, predominant outcrossers dispersed greater numbers of seeds, as their progeny were not affected by inbreeding depression to the same extent as were those of the selfers.

The effects of metapopulation dynamics on evolution at the mating-system locus are complex because they are the result of the joint action of at least three different processes that our simulations have identified. First and foremost, the repeated bottlenecks that occur during the process of colonisation dramatically reduce the effective size of the population (Whitlock and Barton, 1997; Pannell and Charlesworth, 2000); this reduces times to fixation and reduces the efficacy of selection so that fixation probabilities even of selected alleles approach just their initial frequency in the population (Crow and Kimura, 1970). This effect of metapopulation dynamics is largely independent of the mating system as we have modelled it here. Second, the process of colonisation causes lineages to pass through population bottlenecks during which population sizes are small. As our simulations of a finite population have shown, context-dependent mating in small populations alters the mode of self-fertilisation in such a way that alleles for greater selfing experience a fixation bias. We should stress again that this effect is *not* a simple result of selection, as explained above. Finally, frequent population turnover confers a direct selective advantage on facultative outcrossers in our model when selfing results in inbreeding depression. This is simply because outcrossers are able to disperse greater numbers of viable progeny. The result differs from predictions made on the basis of “Baker’s Law” (Baker, 1955, 1967; Pannell and Barrett, 1998), where reproductive assurance through selfing is selected during colonisation if mating is pollen- or mate-limited in obligate outcrossers; our results are more applicable to systems where outcrossing is facultative. Indeed, it is evident that selection for reproductive assurance may not only be a force responsible for the breakdown of outcrossing and the evolution of self-fertilisation, but also one that could lead to the type of facultative, context-dependent, mating system that we have modelled here (e.g., Pannell and Barrett, 1998; Stephenson *et al.*, 2000).

## CONCLUSIONS

The behaviour of both neutral and selected alleles in finite and structured populations has been analysed in much detail (e.g., Wright, 1931; Slatkin and Maruyama, 1975; Slatkin, 1977; Nagylaki, 1982; Whitlock and Barton, 1997), but the effects of population size and metapopulation dynamics on alleles governing the mating system in particular have remained largely unexplored. Our study of the dynamics of a mating-system polymorphism indicates

that these effects may be complex and may differ in interesting ways from those expected for non-mating-system loci. Our model incorporated in a simple way several factors that are thought to be important in mating-system evolution, i.e., inbreeding depression (e.g., Charlesworth and Charlesworth, 1987), pollen discounting (e.g., Nagylaki, 1976; Holsinger *et al.*, 1984; Harder and Wilson, 1998), and modes of selfing (e.g., Lloyd and Schoen, 1992). Our simulations have shown that the influence of these factors on the effective size of a population, i.e., on its susceptibility to genetic drift, may depend in subtle but potentially important ways on the context in which mating occurs. Context-dependent mating may be quite common in self-compatible plants capable of outcrossing, where selfing rates may depend on population size and density. This is particularly expected in wind-pollinated species where the assumptions regarding random mating in small mating neighbourhoods are most likely to be upheld (e.g., Levin and Kerster, 1974; Farris and Mitton, 1984; Wolff *et al.*, 1988; Holsinger, 1992; Chaisurisri *et al.*, 1994; Pannell, 1997), but there is also some evidence for them in insect-pollinated species (e.g., Ellstrand *et al.*, 1978; Burdon *et al.*, 1989; Barrett and Husband, 1990; Widen and Widen, 1990; van Treuren *et al.*, 1991).

Our study has demonstrated an influence of population size and population turnover on the prevalent mode of selfing, and that this in turn may affect the balance between selection and genetic drift in plant populations. Although we have not examined the effect of population size and metapopulation dynamics on the evolution of the mating system (though see Pannell and Barrett, 1998), several models have demonstrated that changes in the mode of self-fertilisation can indeed be important in this regard (e.g., Lloyd, 1979; Schoen *et al.*, 1996) and may potentially alter selection on aspects of reproductive biology such as sex allocation and phenology.

## APPENDIX: RECURSION EQUATIONS FOR THE MODEL

We use the same reasoning to write the recursion equations for  $g'_1$  and  $g'_2$  as was described in greater detail in the text for  $g'_3$ . Recall that in the mixed-mating model, there are broadly three types of matings that can take place: (1) prior self-fertilization, over which plants exercise their own control, at a rate  $s_1$  or  $s_2$ ; (2) outcrossing; and (3) competing selfing (i.e., selfing that can still take place after outcrossing has occurred and pollen discounting has been accounted for). If we let  $g'_{i(\text{prior})}$ ,  $g'_{i(\text{out})}$ , and  $g'_{i(\text{comp})}$  be the numbers of progeny of the  $i$ th genotype

produced in a population by prior selfing, outcrossing and competing selfing, respectively, then  $g'_i$  is the sum  $g'_{i(\text{prior})} + g'_{i(\text{out})} + g'_{i(\text{comp})}$ . These discrete components for  $g'_1$  and  $g'_2$  are written as

$$g'_{1(\text{prior})} = Gs_1(1 - \delta) \left( g_1 + \frac{g_2}{4} \right)$$

$$g'_{1(\text{out})} = G(1 - s_1) \left[ g_1 \left\{ \frac{\left( g_1 - 1 + \frac{g_2}{2} \right) (1 - Ds_1)}{P} \right\} + \frac{g_2}{2} \left\{ \frac{\left( g_1 + \frac{g_2 - 1}{2} \right) (1 - Ds_1)}{P} \right\} \right]$$

$$g'_{1(\text{comp})} = G(1 - s_1)(1 - \delta) \times \left[ g_1 \left\{ \frac{1 - Ds_1}{P} \right\} + \frac{g_2}{2} \left\{ \frac{(1 - Ds_1)/2}{P} \right\} \right]$$

$$g'_{2(\text{prior})} = G(1 - \delta) \frac{g_2}{2}$$

$$g'_{2(\text{out})} = G(1 - s_1) \left[ g_1 \left\{ \frac{\frac{g_2}{2} (1 - Ds_1) + g_3 (1 - Ds_2)}{2} \right\} + \frac{g_2}{2} \left\{ \frac{(g_2 - 1 + g_1)(1 - Ds_1) + g_3 (1 - Ds_2)}{P} \right\} \right] + G(1 - s_2) g_3 \left\{ \frac{\left( \frac{g_2}{2} + g \right) (1 - Ds_1)}{P} \right\}$$

$$g'_{2(\text{comp})} = G(1 - s_1)(1 - \delta) \frac{g_2}{2} \left\{ \frac{1 - Ds_1}{P} \right\}$$

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