A stochastic model of selection on selfing rates in structured populations

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Summary

Previous theoretical studies of the evolution of the selfing rate have shown that mixed mating systems are not evolutionary stable states. Such models have, however, not included the effects of population structure and thus biparental inbreeding together with the evolution of selfing rates and inbreeding depression. In order to examine selection on selfing rates in structured populations, a stochastic model simulating a finite population with partial selfing and restricted pollen and seed dispersal has been developed. Selection on the mating system was followed by introducing modifiers affecting the selfing rate. The major result was that, with density dependent recruitment, a process which maintains the population structure necessary for biparental inbreeding to occur, a mixed mating system could be maintained. This result was associated with an increase of the mutation load with high selfing rates, and the selected selfing rate depended on the degree of population structure rather than on the initial selfing rate. With low dominance of deleterious alleles, complete allogamy can be selected for. Further studies showed that the more general condition of spatial heterogeneity of recruitment can lead to similar results, the most important condition being the maintenance of genetic structure within populations. A brief survey of the empirical literature shows that a positive relationship between the magnitude of inbreeding depression and the inbreeding coefficient within populations has been observed, in support of the present model.

1. Introduction

Genetic models of selection on the selfing rate must include two genetic phenomena that play a critical role in determining the balance between selfing and outcrossing. The first is the twofold advantage of selfing (Fisher, 1941), that is the 'cost of outcrossing' which derives from a doubling of parent–offspring relatedness under uniparental reproduction compared to random outcrossing (Williams, 1975; Charlesworth, 1980; Bulmer, 1982; Uyenoyama, 1984). The second is inbreeding depression, which causes a decrease in the fitness of the progeny of selfers when compared to outcrossers and is due either to the existence of recessive deleterious alleles or to overdominance (Charlesworth & Charlesworth, 1987).

In theoretical models, when inbreeding depression is assumed constant, complete selfing and complete outcrossing have been predicted to be the only two evolutionary stable states expected (Lloyd, 1979), the threshold value above which outcrossing is selected

for being an inbreeding depression of 50% due to the twofold advantage of selfing. More recently, dynamic models, in which the genetic basis of inbreeding depression is specified, i.e. it depends on the mutational or segregational load, have shown the same result (Lande & Schemske, 1985; Campbell, 1986; Holsinger, 1988; Charlesworth *et al.* 1990, 1991, 1992). When selfing and inbreeding depression both evolve, self-fertilization, by increasing the proportion of homozygous loci, leads to the elimination of recessive and partially recessive deleterious alleles; this has been called the 'purging process' (Wright, 1977; Lande & Schemske, 1985). As a population becomes sufficiently inbred, inbreeding depression decreases due to this purging process, and the selfing rate tends toward unity. Such variation in the extent of inbreeding depression causes selection to lead to either complete outcrossing or complete selfing (Lande & Schemske, 1985). Under these models, mixed mating systems that are known to exist in natural populations of many bisexual plants (Stebbins, 1957; Allard, 1975; Jain, 1976; see also Schemske & Lande, 1985; Aide, 1985), and in some hermaphrodite animals

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(Jarne & Charlesworth, 1993) appear only as transient or non-adaptive states. These recent models also show that various kinds of disequilibrium between deleterious alleles and alleles determining the selfing rate can occur and modify the conditions in favour of selfing (Campbell, 1986; Holsinger, 1988; Charlesworth *et al.*, 1990; Uyenoyama & Waller, 1991 *a, b, c*). As a result, dynamic models, allowing the evolution of both the inbreeding depression and the selfing rate, are required when the evolution of the mating system is studied.

Several ecological or supplementary genetical factors have been proposed to be involved in the stability of mixed mating systems (see reviews by Jarne & Charlesworth, 1993; Uyenoyama *et al.* 1993). Among them, population structure may have an important effect on mating system evolution and on the maintenance of intermediate selfing rates (Lloyd, 1980; Uyenoyama, 1986; Waller, 1993). As reviewed by Heywood (1991), allozyme variation within plant populations is often structured in space, presumably resulting from restricted pollen and/or seed dispersal. Due to such restricted gene flow, matings between neighbouring individuals sometimes involve genetically related individuals, a phenomenon that is referred to as 'biparental inbreeding' (Uyenoyama, 1986). With biparental inbreeding, the genetic relatedness between parents and progenies ('fidelity' *sensu* Waller, 1993) is greater than when mating is between unrelated individuals. As a result, the cost of outcrossing and consequently the transmission advantage of selfing is lowered. As shown by Uyenoyama (1986), this introduces the possibility of selection for a mixed mating system even under uniform levels of inbreeding depression. This arises because the parent–offspring relatedness increases with the selfing rate of the population, so that the cost of outcrossing decreases with selfing. This correlation can lead to frequency-dependent selection on selfing under appropriate values of inbreeding depression for different selfing rates (Uyenoyama, 1986). The plausibility of such appropriate values has been questioned. Indeed, inbreeding depression is also expected to affect offspring of biparental inbreeding and to be modified when there is biparental inbreeding. Indeed, biparental inbreeding, as well as selfing, leads to a higher degree of homozygosity compared to random outcrossing and consequently contributes to the purging process; it should thus decrease inbreeding depression. The extent to which biparental inbreeding contributes to the purging process depends on the population size and on the extent to which gene flow is restricted (Waller, 1993). Hence, biparental inbreeding will decrease (1) the cost of outcrossing (which should promote outcrossing), and (2) the magnitude of inbreeding depression (which should promote selfing). The evolutionary stable selfing rates in structured populations are thus of interest, and should be examined in realistic models that incorporate the

genetic basis of inbreeding depression (Campbell, 1986; Uyenoyama, 1986).

The purpose of this study is to develop a stochastic model of populations submitted to restricted gene flow, and to determine conditions under which an intermediate selfing rate could represent equilibrium configurations. A finite and partly selfing plant population, with limited pollen and seed dispersal, is considered. In order to permit correlated variation in the level of inbreeding and the inbreeding depression experienced by the population, individuals' fitness values are determined by numerous loci, subject to partly deleterious mutations. The evolution of the mating system is analysed using modifier loci that alter the selfing rate (see Charlesworth *et al.* 1990, 1991, 1992). Models of geographic structure involving finite populations generally lead to the formation of large clumps of individuals (Felsenstein, 1975) whose distribution varies so that no equilibrium for population structure can be reached. Stability can be obtained using constraints on local density (Felsenstein, 1975; Turner *et al.* 1982). Such constraints were introduced into the present model by density dependent recruitment. In order to ascertain the role of each factor, the outcome of selection on selfing was modelled and compared in three scenarios in which populations were submitted to: [1] restricted gene flow without any density-dependent constraints, [2] density-dependence without restriction on gene flow and, [3] restricted gene flow together with density-dependence.

2. Methods

2.1. *The model*

The computer program simulates a population of N self-compatible hermaphrodite diploid plants, with non-overlapping generations and synchronised flowering periods. These plants are distributed on the intersection points of a grid with L nodes on each of its axes. Only one plant can grow at a single node. The parameter L determines the population density according to density $= N/L^2$, and the population size remains constant through time. The genetic system is composed of a set of bi-allelic unlinked loci. Multilocus genotypes are stored as bit patterns of 0 and 1, such that an individual's genotype is coded for by two sets of words, each set representing a haplotype. This model was written in Turbo Pascal and run on a 486-DX PC. The program is available upon request.

The general design of the model is as follows: as a first step, a fixed initial selfing rate (S_{init}) is imposed so that the population characteristics can reach a quasi-equilibrium. Then, in order to observe selection on the selfing rate in these populations, modifiers of the selfing rate are introduced. These two stages are detailed below as: 'Base population' and 'Runs with modifiers of the selfing rate', as in Charlesworth *et al.* (1992).

2.1.1. *Base population*

The sequence of operations for each generation is that described in Kondrashov (1985). Mutation is followed by reproduction and zygote selection.

(i) *Mutation*

Mutation is modelled by changing the state of individual alleles (bits) from 0 (the wild-type allele) to 1 (the deleterious allele), and the number of mutations occurring each generation is determined by the mutation rate for the whole diploid genome, U. The number of loci per individual is effectively infinite because loci that are fixed for wild-type or mutant alleles are regularly discarded. At equilibrium for the selfing rate, the number of polymorphic loci also reaches a quasi-equilibrium state because on average the number of new loci generated by the mutation process is equal to that discarded after fixation. Fixed loci are scored and taken into account to measure the mean fitness value of the population.

(ii) *Reproduction*

Since the population size (N) remains constant, N offspring are produced each generation from the N individuals of the previous generation.

(a) *Choice of the parents*

To achieve a fixed selfing rate (i.e. a proportion S_{init} of zygotes produced by selfing), the production of each zygote begins by drawing a random number between 0 and 1: self-fertilization occurs when this number is lower than S_{init}, and cross-fertilization otherwise. For selfed zygotes, only one parent is chosen, while a second parent has to be chosen for cross-fertilization to occur. We used 4 different models to choose parents in the case of outcrossing. In all the cases, the sampling of parents is with replacement, such that one individual can have more than one offspring. The first 3 mating processes are now described (the fourth will be explained in section 2.3. following explanations of the selection procedure involved).

Model [1]: *limited pollen and seed dispersal.* The female parent is drawn at random from the population. The male parent is chosen depending on *Mdisp*, the pollen dispersal distance (a fixed parameter for the whole population). As in Turner *et al.* (1982) and Rohlf & Schnell (1971), males are chosen from those plants whose distance from the mother is smaller than *Mdisp*. Calling n the number of plants in this area, they each had a probability of $1/n$ of being chosen as male parent in any given mating. When this area is unoccupied, males are chosen within a distance of 2*Mdisp, and so on (see Fig. 1). When *Mdisp* = L, the pollen dispersal distance is not limited, and our results can be compared with those obtained by Charlesworth
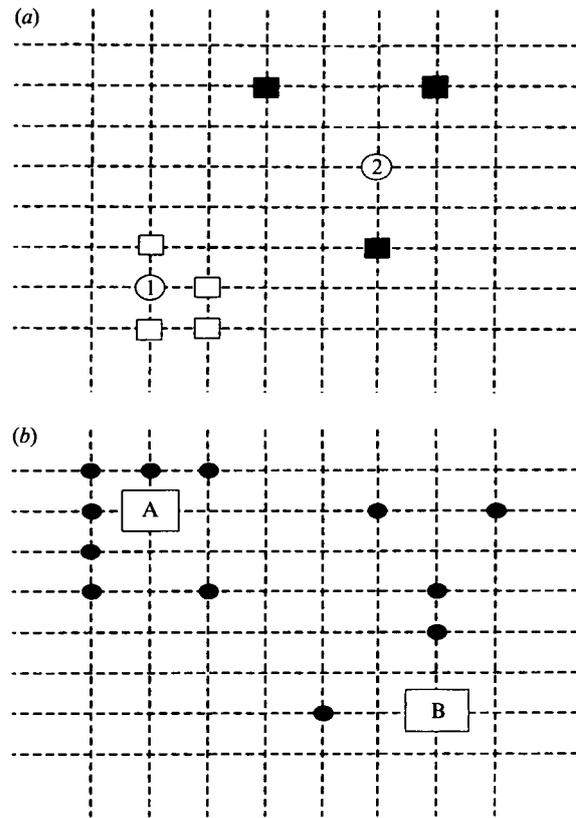

Fig. 1. Mating schemes. (*a*) Four plants are located at the pollen dispersal distance of mother plant 1, and the pollen dispersal distance *Mdisp* is equal to 1. Each of these plants has a probability of 0·25 to be the male parent (■, □). For the mother plant (○) 2, no plants are at the pollen dispersal distance. In that case, the male parent is chosen among the three plants located at twice the pollen dispersal distance (■), each having a probability of 1/3 of being chosen. (*b*) The recruitment probability *area* of a given individual (●) depends on the number of plants located at the nearest distance around it. Individual A has an *area* equal to 1/5, because five plants are located within a distance of one unit. For individual B, *area* depends on the number of plants located at a distance of two units since no plants are at a distance of one unit. *Area* = 1/2.

et al. (1992) for partly selfing population with random outcrossing.

Model [2]: *density-dependent fertility.* Each generation, a spatial parameter denoted *area* is first calculated for each individual. Each unoccupied node of the grid has one or more occupied nodes to which it is closest. For an individual I, *area* (I) is the number of unoccupied nodes to which it is closest. If there are n individuals equally close to a particular unoccupied node, *area* for each of these individuals is incremented by $1/n$. Hence, *area* is inversely proportional to the number of plants located around a given individual (see Fig. 1 *b*), i.e. it increases with isolation. We used these values as the probabilities that particular individuals would be chosen as female parents. In this way, for each zygote, a random number z is drawn, and the first randomly drawn individual whose *area* is

higher than z is chosen as the mother plant. This procedure increases the reproductive probability of individuals occurring at low density, and precludes the formation of large clumps. For outcrossing events, the male parent is chosen at random from the whole population.

Model [3]: both limited pollen and seed dispersal and density-dependent fertility. In this case, female parents are selected as in model [2] and, for a given female parent, the choice of male parent follows the pollen dispersal distance procedure as described in model [1].

When the two parents are chosen, the offspring genotypes are determined by drawing at random an allele from each locus of each parent (for selfing, the two haplotypes come from the female parent). Free recombination was assumed among loci.

(b) Position of the zygote

At the beginning of each base population, the individuals are randomly located on the grid. To simulate restricted seed dispersal (models [1] and [3]), the position of each new zygote is chosen depending on the position of the mother and on the seed dispersal distance parameter, *Fdisp*. The offspring position is drawn from a normal distribution centred on the mother's position, with a variance equal to *Fdisp*. The dispersal direction was chosen at random among the unoccupied positions in the eight possible directions around the mother. For individuals located close to the edges, the same process was followed with the possible positions which were located outside the grid being considered as occupied sites. In model [2], i.e. without any restriction in seed dispersal, $Fdisp = \infty$.

(iii) Selection

We assume a multiplicative selection regime with the same selection parameters at all loci. The fitness of a zygote with j mutations in the homozygous state and i in the heterozygous state is given by the following expression:

$$W_{i,j} = (1-s)^j \times (1-hs)^i,$$

where s is the selection coefficient against homozygotes for a mutant allele, and h is the dominance coefficient of this allele. Once the zygote fitness is calculated, a random number between zero and one is drawn: the zygote survives when its fitness is higher than this number. This process of parental choice, fitness calculation and selection is repeated until the number of surviving zygotes reaches N.

To allow mutations to build up, and to reach a steady state between mutation and selection, 200 to 400 generations were necessary. Thus, for all the set of parameters studied, this 'base population' phase was initially run for 400 generations. At this point, various population variables which are described below in the 'measured values' paragraph, could be calculated.

2.1.2. Runs with modifiers of the selfing rate

These runs are similar to those carried out by Charlesworth *et al.* (1992), except that the selfing rate is determined by alleles at 10 bi-allelic ($+$ and $-$) loci (only one locus was used by Charlesworth *et al.* 1992) with additivity between loci and codominant effects of alleles. The individual selfing rate is defined as the number of $+$ alleles divided by 20, and therefore varied between 0 and 1 by increments of $1/20$. At the beginning of these runs, the genotypes at these 'selfing rate loci' were determined such that the selfing rate of each individual was the mean selfing rate of the corresponding base population. Mutations between the two allelic states occurred each generation at the rate *uself*, which is defined as the mutation rate per locus that determines the selfing rate. The other processes were as described above for the base population. This second phase was run at the most for 4000 generations. When the selfing rate was not fixed at 0 or 1 after 2000 generations, the mean selfing rate in the population was measured each 10 generations in order to determine the mean values and standard deviations of the quasi-equilibrium selfing rate. To check for stochasticity, 10 base populations each followed by a 'run with modifiers of the selfing rate' were compared for each set of parameters.

2.2. Studied parameters and measurements

2.2.1. Parameter values

We used the selection parameters $s = 0.1$ and $h = 0.2$ throughout, except where otherwise stated. These values are based on the scanty data, obtained on *Drosophila* (Simmons & Crow, 1977), which suggest that mutations with slight effects on fitness are the commonest type of deleterious mutations. The mutation rate U assumed per diploid genome per generation was 1 (also estimated on *Drosophila*, Simmons & Crow, 1977; Houle *et al.* 1992). Similar values have also been found in plants (Crow, 1993).

As the individuals are distributed on a grid, the area or distance parameters are expressed in spatial units (a unit corresponding to $1/L$). The size of the population (N) was 200. Two values of L were studied: $L = 24$ (density $= N/24^2 = 0.35$) and $L = 48$ (density $= 0.08$), and in both cases, *Mdisp* took the values 1 or L, and *Fdisp* the values 1, 2 and L, respectively.

In runs with modifier alleles, the mutation rate per generation and per locus determining the selfing rate, *uself*, was fixed at 10^{-3} (leading to, on average, 2 mutations per generation in the whole population over all loci that determine selfing rate, $N \times 10 \times 10^{-3}$).

2.2.2. Measured values

For the fixed initial selfing rate, the fitnesses of selfed and outcrossed progenies were recorded in the base populations after 400 generations, and were used to

calculate the mean fitness and mean inbreeding depression of the populations. Inbreeding depression was defined as: $\delta = 1 - W_s/W_x$, where W_s and W_x are the average fitnesses of selfed and outcrossed progenies respectively (outcrosses are here considered in the defined neighbourhood, i.e. for the pollen and seed dispersal distance of the corresponding population).

(i) *Population structure*

In order to examine the genetic structure of the modelled populations and also to estimate the relationship between population structure and selfing rates, 10 neutral bi-allelic loci were introduced into the populations to measure F-statistics. These loci were submitted to the same mutation process as loci determining fitness (see the mutation process above). The total deficit of heterozygotes from Hardy–Weinberg, F_{IT}, was calculated over all individuals in the population as:

$$F_{IT} = 1 - \frac{\text{observed heterozygosity}}{\text{expected heterozygosity}},$$

where the expected heterozygosity is $(1 - \Sigma p_i^2)$ and p_i is the frequency of allele i in the population. One can then obtain an estimate of the population structure which results from biparental inbreeding by estimating F_{ST} according to

$$F_{ST} = 1 - \frac{1 - F_{IT}}{1 - F_{IS}},$$

where $F_{IS} = Self/(2 - Self)$ (Crow & Kimura, 1970), and *Self* is the realized selfing rate.

In regard to Wright's F-statistics, in the present case of bi-allelic loci, F_{IT} corresponds to the total deficit of heterozygotes, while F_{IS} and F_{ST} correspond to the deficit of heterozygotes due to selfing and to isolation by distance respectively (Wright, 1969, vol. 2). The cost of outcrossing (c) in the presence of biparental inbreeding can be estimated as $(1 - r)/2$, where r is the relatedness between outcrossed individuals. r is related to F_{ST} through the formula: $r = (2 \times F_{ST})/(1 + F_{ST})$ (Michod & Hamilton, 1980).

2.2.3. *Testing the model*

For *Mdisp* $= L$ and *Fdisp* $= \infty$ (pollen and seed dispersal distances are not limited) and without density dependence, the modelled population corresponds to a finite population with partial selfing and random outcrossing. Mean fitness, mean inbreeding depression and selection on the selfing rate could thus be compared to results of previous stochastic calculations (Charlesworth *et al.* 1990, 1992).

2.3. *Further study of the effect of the density-dependent recruitment*

When recruitment of the parents depends on *area* (model [2] and [3]), the reproductive success of an

individual (defined as the number of offspring it contributes to the next generation) depends on two factors. First, the mutational load: the lower the number of deleterious mutations carried, the higher the survival probability of the offspring. This component defined as simply $W_{i,j}$ above will be termed the 'genetic fitness' of an individual. Second, the *area* value estimates the probability of an individual being selected as a mother plant. This depends directly on the density of surrounding plants. The correlation between these two selective factors (*area* and $W_{i,j}$) was calculated every 20 generations.

Model [3*]. We examined the influence of other factors that can maintain a stable population structure, namely space and time-dependent selection. Moreover, due to the density-dependent constraint, there are both spatial and temporal correlations between the individuals for their *area* value. The spatial correlation is due to the fact that two neighbours experience similar densities. The temporal correlation exists because, after selection, a zygote is expected to be isolated when its parents are isolated (because inbreeding depression reduces the progeny of a selfer). Because *area* is a component of reproductive success (it determines the recruitment probability of plants as mother), density-dependence leads to spatial and temporal correlations for recruitment, and hence both correlations affect the maintenance of population structure. In order to assess the role of both spatial and temporal correlations, the recruitment parameter *area* was replaced by a sinusoidal function that allows for variation in space and time:

$$area(I) = f(x, y) = a + \frac{\sin(2\pi k x') \times \sin(2\pi k y')}{b},$$

where $x' = 1 - x/L$ and $y' = 1 - y/L$, x and y, the coordinates of individual I on the two axes of the grid (a) and (b), were fixed such that values of *area* varied between 0 and 1 with a variance similar to that obtained in model [3] (see Appendix). This function allows for the influence of the spatial or the temporal correlation to be made independently of one another. Through modification of the parameters as described in the appendix, complete runs were made (1) with temporal and spatial correlations, (2) without temporal correlation and, finally, (3) without spatial correlation.

3. Results

3.1. *Random outcrossing model*

The model was checked by simulating a partly selfing population in which outcrossing occurs between unrelated individuals (*Fdisp* $= \infty$, *Mdisp* $= L$). This model will be referred to as the *random outcrossing model*. Mean inbreeding depression values observed in the corresponding base populations with various initial selfing rates (*Sinit*) were in agreement with

Charlesworth *et al.* (1992) who performed simulations for populations of 400 individuals, with $s = 0.1$, $h = 0.2$, $U = 1$ (see fig. 2 in their paper). As expected, complete outcrossing and complete selfing are the only two stable states observed, and the selfing rate selected depends on the initial selfing rate experienced by the population. With our parameters, for *Sinit* values above 0·05, the populations evolve towards complete selfing.

3.2. *Model [1]: restricted gene flow alone*

3.2.1. *Selection on the selfing rate*

Figure 2*a* shows the evolution of the selfing rate in populations with different population structure parameters. As in the *random outcrossing model*, complete outcrossing and complete selfing are the only stable states observed, and the final selfing rate depends on the initial selfing rate of the population. For low selfing rates and large structure parameters ($L = 48$, *Fdisp* = *Mdisp* = 1), gene flow restriction gives a slight

Fig. 3. Mean inbreeding depression observed in base populations with different initial selfing rates. (*a*) Dotted lines represent random outcrossing populations, and full lines represent populations submitted to restricted gene flow (model [1]) with pollen and seed dispersal distances, *Mdisp* and *Fdisp* = 1 and $L = 48$. Standard deviations are reported around the means. (*b*) Populations are submitted to both restricted gene flow and density dependence (model [3]). In dotted lines, *Mdisp* = 1, $L = 24$ and *Fdisp* = 1. In full lines, $L = 48$ and square symbols for *Fdisp* = 1 and diamond-shaped symbols for *Fdisp* = 2. For clarity of the figure, standard deviations have not been reported: S.D. values ranged between 0·05 and 0·005. Arrowheads indicate the selected states.
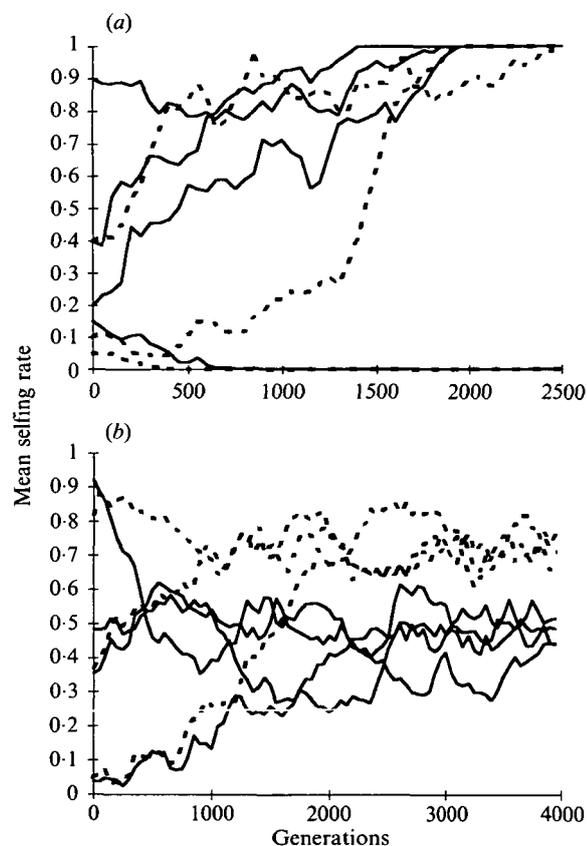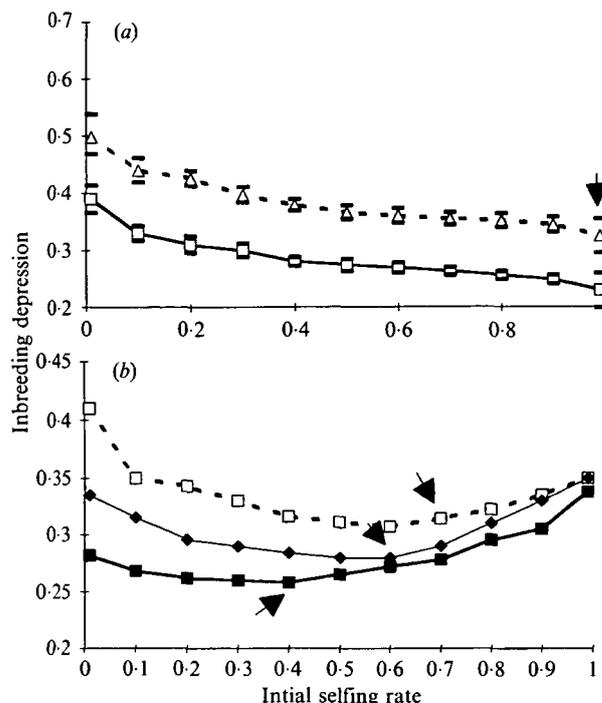

Fig. 2. Evolution of the mean population selfing rate according to gene flow restriction and density dependence imposed in the population. The selfing rate at generation 0 is the selfing rate in the corresponding base population. In (*a*), dotted lines correspond to randomly outcrossing populations, and full lines to populations submitted to restricted gene flow (model [1]), i.e. the dispersal distance of pollen and seed, respectively *Mdisp* and *Fdisp* = 1, and the number of nod on the grid, $L = 48$. In (*b*), populations are submitted to both restricted gene flow and density dependent recruitment (model [3]): *Mdisp* = *Fdisp* = 1 and $L = 24$ (dotted lines) or $L = 48$ (full lines).

advantage to outcrossing since the value of the initial selfing rate above which selfing was favoured was approximately 0·15 instead of 0·05 for the *random outcrossing model* (with $h = 0.2$, $s = 0.1$ and $U = 1$ in both cases).

3.2.2. *Inbreeding depression*

As expected, inbreeding depression decreases (1) with increasing selfing but also, for a given selfing rate, with increasing restriction in gene flow (Fig. 3*a*). In parallel, the number of mutations per individual decreases, not only with increasing selfing rates, but also with higher levels of biparental inbreeding for comparable selfing rates (Fig. 4). Hence, the purging process is as expected enhanced through biparental inbreeding.

3.2.3. *Population structure*

F_{ST} values indicate that even with a strong restriction on gene flow and low density, the population remains almost unstructured. For $L = 48$ and *Fdisp* = *Mdisp* = 1, mean F_{ST} values ranged from -0.05 (mean
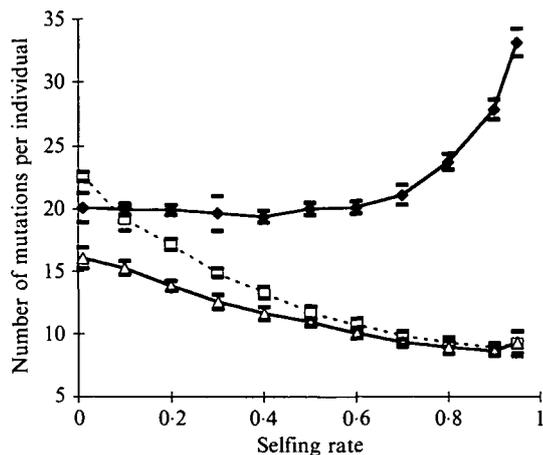
Fig. 4. Mean number of mutations per individual in 'base populations' with different selfing rates and for different cases of gene flow restriction and density dependance: square symbols correspond to randomly outcrossing populations, i.e. model [1] with $Mdisp = L$ and $Fdisp = \infty$, triangle symbols to populations submitted to restricted gene flow only, i.e. model [1] with $Mdisp = Fdisp = 1$ and $L = 48$, and diamond-shaped symbols to populations submitted to both restricted gene flow and density dependance, with $Mdisp = Fdisp = 1$ and $L = 48$.

standard deviation between generations and averaged among 10 runs (S.D.) = 0·43 for a $S_{init} = 0·9$) to 0·18 (S.D. = 0·10; for $S_{init} = 0·1$) in the base populations. This should be compared to the *random outcrossing case* (with $Mdisp = L$, $Fdisp = \infty$) where F_{ST} is approximately 0 and S.D. ranged from 0·004 to 0·19 depending on the initial selfing rate (S_{init}). Finally, the correlation between population structure F_{ST} and the realized selfing rate *Self* is: $-0·76$ ($P < 0·05$) and $-0·63$ ($P > 0·05$) for $L = 48$ and $L = 24$ respectively ($Fdisp = Mdisp = 1$).

3.3. *Model [2]: density-dependent fertility*

The selfing rates selected in this case are similar to those obtained in the *random outcrossing model*. Whatever the density of the population ($L = 24$ or 48), complete selfing is selected for if the initial selfing rate is above 0·05, and complete outcrossing in the alternative case. Thus, density-dependence alone had no effect on the selected selfing rate compared to the *random outcrossing model*.

The inbreeding depression experienced by such populations as well as the mean numbers of homozygous and heterozygous mutations per individual and the population mean fitness are also only slightly different from that obtained with the *random outcrossing model*. As expected since gene flow is not limited, the average value of F_{ST} is around 0. It ranges between $-0·3$ and 0·13 (for selfing rate between 0·9 and 0·1) with large variations between generations and between runs (with standard deviations as large as 0·28). The correlation between F_{ST} and *Self* is equal to $-0·75$ ($P < 0·05$) and $-0·77$ ($P < 0·05$) for $L = 48$ and $L = 24$ respectively.

3.4. *Model [3]: restricted gene flow and density-dependent recruitment*

3.4.1. *Selection on the selfing rate*

In this case, the selfing rate reaches intermediate values and then varies slightly around this equilibrium value (Fig. 2b). The final selfing rates were around 0·7 (S.D. = 0·06) and 0·85 (S.D. = 0·08) when $Fdisp = 1$ and 2 respectively, with $L = 24$ and $Mdisp = 1$, and around 0·45 (S.D. = 0·05) and 0·55 (S.D. = 0·045) for the same values of $Fdisp$, with $L = 48$ and $Mdisp = 1$. The selfing rate selected now depends on the population density and not on the initial selfing rate in the population. In particular, the lower the density of the whole population, the lower the final selfing rate. In other words, the stronger the effects of density, the more outcrossing is favoured.

3.4.2. *Inbreeding depression and mutation load*

For a given initial selfing rate, lower density causes lower inbreeding depression (Fig. 3b). For a given set of population structure parameters (L, $Fdisp$, $Mdisp$), inbreeding depression may vary in two ways as the selfing rates of the base population changes. For selfing rates ($Sinit$) below the selfing rate selected for inbreeding depression decreases with selfing whilst for selfing rates above the selected value, inbreeding depression actually increases with increased selfing (Fig. 3b). The increased inbreeding depression is associated with an increase in the genetic load, particularly at high selfing rates, as shown by the higher number of deleterious mutations per individuals although no fixation occurs (Fig. 4). This shows that for high selfing rates and when both biparental inbreeding and density dependence are implied, the purging process is less effective. This result suggests that, in runs with modifiers, the process directing the evolution of selfing is the occurrence of such a minimum value of inbreeding depression. Indeed, selfing evolves towards the value for which inbreeding depression is the lowest (Fig. 3b). One must, however, notice that the final selfing rate is slightly higher than this minimum value. This suggests that a supplementary process in favour of selfing is also involved in the selection of the selfing rate.

3.4.3. *Population structure*

In contrast to model [1], isolation by distance due to restricted gene flow remains stable along generations: F_{ST} decreases with density and with dispersal distances (see Table 1). These values are well conserved over generations since the standard deviations (over more than 100 generations) ranged between 0·04 and 0·1 for the runs described above. Finally, the correlation between F_{ST} and *Self* is: $-0·66$ ($P > 0·05$) and $-0·29$ ($P > 0·40$) for $L = 48$ and $L = 24$ respectively (with $Mdisp = Fdisp = 1$).

Table 1. *Comparative values of population structure (F_{ST}), relatedness (r), cost of outcrossing (c), inbreeding depression (δ) and selected selfing rates in runs with different sets of parameters (model [3])*

	F_{ST} (S.D.)	r	Cost of outcrossing c	Observed δ (S.D.)	Final selfing rate (S.D.)
$L = 24 - s = 0.1 - h = 0.2$					
$FDisp = 1$	0.30 (0.05)	0.46	0.27	0.31 (0.01)	0.7 (0.06)
$FDisp = 2$	0.26 (0.04)	0.37	0.31	0.32 (0.01)	0.85 (0.08)
$FDisp = 4$	0.10 (0.03)	0.18	0.41	0.34 (0.02)	1
$FDisp = 10$	0.02 (0.04)	0.04	0.48	0.35 (0.01)	1
$L = 48 - s = 0.1 - h = 0.2$					
$FDisp = 1$	0.6 (0.04)	0.75	0.12	0.27 (0.01)	0.45 (0.05)
$FDisp = 2$	0.55 (0.03)	0.71	0.14	0.29 (0.01)	0.55 (0.04)
$FDisp = 4$	0.30 (0.02)	0.46	0.27	0.32 (0.01)	0.75 (0.06)
$FDisp = 10$	0.16 (0.03)	0.32	0.34	0.34 (0.02)	1
$L = 48 - s = 0.2 - h = 0.2$					
$FDisp = 1$	0.71 (0.02)	0.83	0.08	0.29 (0.02)	0.3 (0.06)
$FDisp = 2$	0.62 (0.04)	0.76	0.12	0.31 (0.01)	0.45 (0.07)
$FDisp = 4$	0.42 (0.03)	0.59	0.20	0.33 (0.03)	0.7 (0.04)
$FDisp = 10$	0.23 (0.03)	0.37	0.31	0.36 (0.02)	0.9 (0.05)
$L = 48 - s = 0.5 - h = 0.2$					
$FDisp = 1$	0.82 (0.03)	0.90	0.05	0.33 (0.01)	0.6 (0.04)
$FDisp = 2$	0.71 (0.02)	0.83	0.08	0.35 (0.02)	0.72 (0.05)
$FDisp = 4$	0.52 (0.02)	0.71	0.14	0.36 (0.01)	1
$FDisp = 10$	0.30 (0.03)	0.46	0.27	0.37 (0.03)	1
$L = 48 - s = 0.2 - h = 0.1$					
$FDisp = 1$	0.67 (0.02)	0.80	0.10	0.37 (0.01)	0
$FDisp = 2$	0.53 (0.02)	0.69	0.15	0.39 (0.01)	0
$FDisp = 4$	0.37 (0.02)	0.54	0.23	0.42 (0.01)	0.2 (0.03)
$FDisp = 10$	0.2 (0.03)	0.33	0.34	0.52 (0.02)	0.7 (0.04)

r and c are calculated as defined in the methods section and using the mean F_{ST} values. Mean F_{ST} and mean δ are measured for the corresponding final selfing rate; standard deviations (S.D.) are calculated over 10 performed runs for each set of parameters (standard deviations within runs and between generations are approximately 0.10 for F_{ST} values and between 0.005 and 0.06 for δ). (s, the selection coefficient; h, the dominance coefficient; L, the number of nodes on the grid and *FDisp*, the seed dispersal distance.)

3.4.4. *Further characteristics of this third model*

The two components of the reproductive success of an individual, i.e. the *area* value and the *genetic fitness* ($W_{i,j}$) were negatively correlated (for example, $Cor(area, W_{i,j}) = -0.20$, $P < 0.01$, for $L = 48$ and $Fdisp = Mdisp = 1$). This means that isolated individuals have larger mutation loads than average.

Table 1 gives the relationship between the equilibrium selfing rate and population structure (F_{ST}) for different selection parameters (s, h). With h values below 0.15, complete outcrossing can be selected for and this was associated with higher inbreeding depression values (see Table 1 for $h = 0.1$). In most of the cases leading to an intermediate selfing rate, inbreeding depression was lower than one half, the threshold value under which selfing should be favoured in random outcrossing populations. For fixed selection parameters and density, the magnitude of inbreeding depression only slightly decreased with increasing population structure. In contrast, the cost of outcrossing is highly reduced when the population structure increases. The result of these two effects is that inbreeding depression always remains higher than the cost of outcrossing so that selection for

outcrossing is expected (Table 1). One can notice that the level of inbreeding depression is clearly not sufficient to allow prediction about the direction of selection. For a given set of the parameters that characterize deleterious effects (h, s, U), inbreeding depression is a decreasing function of the population structure, and for varying restrictions on gene flow (*DispF*), this is associated with a clear negative correlation between the selected selfing rate and the population structure (Fig. 5). The more the gene flow is restricted, the more selection in favour of outcrossing is observed.

3.5. *Model [3*]: spatial and/or temporal correlations*

To analyse the role of spatial correlations, we define the recruitment probability (*area*) as a sinusoidal function of the individual's position (see methods). In this case, depending on the values of the parameters, there can be either a spatial or else a temporal correlation (see appendix). With $k = 4$ and $Fdisp = 1$ (i.e. temporal and spatial correlation for the recruitment probability) the selfing rate selected for is 0.5. With only temporal correlations ($k = \infty$ and $Fdisp = 0$), the selfing rate evolves towards 1, whatever
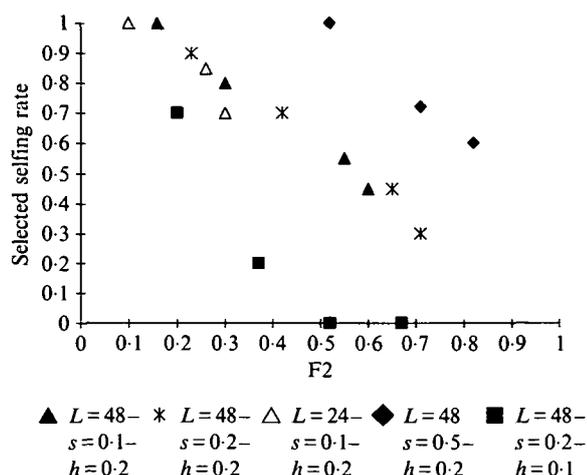
Fig. 5. Relationship between population structure and selected selfing rates for five sets of parameters. For one set of parameters, reported values correspond to *Fdisp* = 1, 2, 4 and 10 with decreasing values of F_{ST}.

the initial selfing rate and there is no isolation by distance ($F_{ST} = 0$). In contrary, spatial correlations alone (when *Fdisp* = ∞) generate an intermediate selfing rate of 0·90. In this case, F_{ST} remains around 0·15 over many generations (S.D. = 0·07), and there is a negative correlation between the '*genetic fitness*' and the '*new area value*': $Cor('newarea', W_{i,j}) = -0.17$ ($P < 0.01$).

4. Discussion

In contradiction to some previous theoretical studies on the evolution of the selfing rate showing that mixed mating could not represent stable states (Lande & Schemske, 1985), the study presented here shows that population structure due to biparental inbreeding can select for mixed mating systems, as also previously shown by Uyenoyama (1986). Restricted gene flow was, however, not sufficient to maintain intermediate selfing rates. In order to find the conditions allowing mixed mating systems to be stable states, we have examined the effects of the following factors on the evolution of selfing: inbreeding depression, cost of outcrossing and genotypic associations between fitness loci and loci controlling the selfing rate (see Uyenoyama & Waller, 1991*a*) in populations of different structures.

4.1. *Selection on the selfing rate in the absence of density-dependence*

In the absence of density-dependence (model [1]), the occurrence of biparental inbreeding still causes an outcome of either complete outcrossing or complete selfing, as has previously been observed in simulations of partly selfing populations with random outcrossing. When matings occur between relatives, two conflicting processes may occur: a decrease of inbreeding depression and a decrease of the cost of outcrossing

(see Introduction). Despite the fact that with biparental inbreeding alone (no density dependence), the expected decrease of inbreeding depression was observed (which should favour selfing), the evolution of modifiers of the selfing rate shows that restriction of gene flow continues to favour outcrossing. Indeed, compared to the case of random outcrossing, the threshold value under which outcrossing was favoured was slightly higher in the case of restricted gene flow (*Self* = 0·15, instead of 0·05 with the same parameter values except for that for gene flow). Thus, despite a decrease in the level of inbreeding depression, a decrease in the cost of outcrossing can counterbalance the expected selection for higher selfing.

Three reasons can account for the fact that the occurrence of biparental inbreeding cannot by itself lead to intermediate stable selfing rates in the present model. First of all, stable significant population structure was not maintained in the present model. F_{ST} (as measured over neutral loci), and consequently r, the relatedness between individuals, was low and highly variable between generations, even with very limited dispersal distance, showing that the population structure was not maintained. When migration is restricted, in the absence of any process that regulates the density of individuals, the development of large unstructured clumps is expected (Rohlf & Schnell, 1971; Felsenstein, 1975). What is important here is that, although purging occurs (and thus inbreeding depression is reduced) due to biparental inbreeding, the predicted decline in the cost of outcrossing will not necessarily occur, because $c = (1 - r)/2$. In our model, an increase of population structure (F_{ST}) with selfing, a necessary condition to have frequency-dependent selection on selfing, was never observed. Instead, we observed decreased population structure, which can be explained by the fact that two neighbours that outcross are more likely to have related ancestors that intercrossed and hence to be genetically related, than is the case for two neighbours that self. Finally, since the magnitude of inbreeding depression is assumed to be dependent on the degree of relatedness of the cross-fertilization parents, inbreeding depression also depends and affects biparental inbreeding. As a result, the magnitude of inbreeding depression in the population decreases and this represents a pre-adaptation to selfing (Uyenoyama, 1986), a process which could limit the possibility of intermediate selfing rate to be maintained. Hence, the required conditions proposed by Uyenoyama (1986) do not hold in our model.

4.2. *Maintenance of intermediate selfing rates in the case of density-dependence*

Introducing density-dependence proved to be necessary to create a stable population structure, but was not sufficient on its own (model [2]). In this model, inbreeding depression remained a decreasing function

of the selfing rate, and neither the magnitude of inbreeding depression nor selection on selfing rate are different from those observed in panmictic populations. The result that selection leads to either complete outcrossing or complete selfing disappears only when both biparental inbreeding and density-dependence are combined within populations (model [3]). The necessity of such a combination can be considered as an illustration of the rule that for kin selection to occur, there must exist some density regulation at the scale at which genetic structures occur (Kelly, 1994).

An intermediate selfing rate is selected for, which depends on the population density and on how gene flow is restricted, rather than on the selfing history of the population. For a given set of parameters (*L*, *DispM*, *DispF*) the final selfing rate is the same whatever the initial selfing rate. The presence of selection for an intermediate selfing rate is interpreted as being due to the fact that at certain selfing rates, inbreeding depression increases with selfing (see Fig. 3*b*), and prevents the fixation of purely selfing lines. The possibility of selection for intermediate selfing rates due to an increase of inbreeding depression with selfing has been already proposed (Lloyd, 1980). In this model, it was assumed that seed-set of an individual increases with its selfing rate and that inbreeding depression increases with density. As a result, an increase of selfing is associated with an increase of inbreeding depression. The advantage of outcrossing was thus, as in our model, density-dependent so that intermediate selfing rates could be selected for. However, the two assumptions (higher seed-set of selfers and density-dependent inbreeding depression) are not required in our model, and the final relationship which is expected between the selected selfing rate and the density of the population is inverse (see Table 1) to that expected in the model of Lloyd (1980).

4.3. *Increase of inbreeding depression with biparental inbreeding and density-dependence*

Although the mutation load decreases with inbreeding in large panmictic populations, it increases with inbreeding in small populations (see table 4 in Charlesworth *et al.* 1993). In structured populations, selection operates both within subgroups that contain related individuals and between these subgroups. The net outcome in a large structured population – increase or decrease of the mutation load with inbreeding – will depend on the precise modalities of the selective regime (see the verbal model proposed by Waller, 1993, p. 111). To explain the observation that, in the present model, the mutational load increases with selfing, one has to consider the variance in reproductive success of the different genotypes present in the population. There are two components of

reproductive success in populations submitted to restricted gene flow and density-dependence: individuals' mutational loads and their local densities. These two components are negatively correlated because individuals with high selfing rates reproduce less successfully due to inbreeding depression, and thus their offspring (which tend to have high selfing rates), are more likely to be isolated than outcrossers. Hence, selfers are less fit and more isolated, and outcrossers have higher local density and higher fitness. As a result, the correlation between the reproductive success and the mutational load is expected to be reduced. Indeed, the regression coefficient β of reproductive success (i.e. number of offspring an individual produces) on genetic fitness ($W_{i,j}$) is equal to 0·055 ($P > 0·50$) in the case of density-dependence (model [3]), while $\beta = 0·27$ ($P < 0·01$) and 0·33 ($P < 0·01$) in the *random outcrossing model* and in model [1] respectively.

When the selective regime is such that the reproductive success of an individual is independent of parental genotype and hence of its mutational load, the purging process is not expected to occur, and instead the mutation load increases with inbreeding (intra-family selection; Couvet & Ronfort, 1994). The analytical resolution of the one-locus model of deleterious mutations shows that in such a selective regime and with biparental inbreeding, an intermediate selfing rate exists that minimizes the frequency of deleterious alleles and the load (Couvet & Ronfort, submitted). The absence of or the very low correlation between the individual's reproductive success and their mutational load observed in model [3] suggests that intra-family selection is at least partly present in this model and is responsible for the increase of inbreeding depression with high selfing rates.

4.4. *The relationship between inbreeding depression and the cost of outcrossing*

In the model presented here, the selfing rate that is selected for depends on the level of population structure but also on the magnitude of deleterious effects and their dominance (see Table 1). In accordance with theory, this selfing rate decreases when population structure increases (and thus the cost of outcrossing decreases). Also as expected, the magnitude of inbreeding decreases with increasing population structure. The quantitative agreement between the cost of outcrossing and the magnitude of inbreeding depression is, however, less good. As shown in Table 1, the magnitude of inbreeding depression is always lower than the expected threshold value (i.e. the cost of outcrossing), so that in all the cases, selection for a lower selfing rate is expected. As a result, the only prediction is that in the limited extent of a given set of selection parameters, increasing levels of outcrossing are expected with increasing population

structure. The discrepancy observed between the cost of outcrossing, the magnitude of inbreeding depression and the expected direction of selection on the selfing rate has also been documented in previous models concerned with the evolution of selfing (without biparental inbreeding) where the observed threshold value of inbreeding depression is higher than the expected one, i.e. $\delta = 1/2(r = 0)$. Associations between fitness loci and modifier loci are thought to account for this discrepancy (Campbell, 1986; Holsinger, 1988; Uyenoyama & Waller, 1991 a), and should also be present in our model. Since such associations are expected to favour selfing, they could account for the difference we observed between the selected selfing rate and the selfing rate for which the inbreeding depression was minimal (see Fig. 3 b).

4.5. Relevance of the results

To generate mixed mating systems, the main condition here is the occurrence of population structure. Low neighbourhood size is common in animal pollinated plants where the foraging behaviour of pollinators creates limited pollen dispersal (Levin & Kerster, 1969; Schaal, 1980; Schmitt, 1983). Seed dispersal on the other hand has been shown to be limited, especially in dense populations (Levin & Kerster, 1968; Schaal, 1975). Local mating is also common in animal populations, particularly for sessile and sedentary organisms (Knowlton & Jackson, 1993; Grosberg, 1991), but also for organisms of high mobility (Endler, 1977). Based on a survey of the plant literature, Loveless & Hamrick (1984) have shown that F_{ST} values range between 0·006 and 0·372, with a mean value of 0·02 for mixed mating species (see also Heywood, 1991). The degrees of population structure required for our model are thus high compared to empirical data (for example, $F_{ST} = 0·6$ for selection of a selfing rate of 0·45).

We tried to find more general conditions for the maintenance of intermediate selfing rates. With spatial heterogeneity of fitness (the recruitment probability) instead of a density-dependent constraint (which generates spatial and temporal correlations for fitness between individuals), population structure and mixed mating systems were maintained. In natural populations, spatial heterogeneity of resources, which can lead to significant local genetic differentiation (Turkington & Harper, 1979; Gehring & Linhart, 1992), is a well-known phenomenon, as is density-dependence (Antonovics & Levins, 1980; Van Treuren *et al.* 1993). This suggests that quite general conditions that lead to populations being structured might result in the maintenance of intermediate selfing rates. In this case, intermediate selfing rates could possibly be maintained with lower *Fst* values, compatible with published data (F_{ST} values around 0·2 were sufficient). In the present framework, on conclusion is that biological mechanisms that affect population structure will also modify the reproductive system. For example, higher density of flowering plants results in a decrease of the flying distance of pollinators and thus to lower neighbourhood area (Fenster, 1991). In this case, according to our model, a decrease of density is expected to lead to selection for a lower selfing rate. Changes in the reproductive system may also occur when new habitats are occupied, as a result of changes in density and neighbourhood sizes, due for example to modifications of the guild of pollinators or the availability of resources in the habitat. Such conditions could lead to the evolution of selfing, not as it is usually proposed due to variation in the proportion of pollen from other plants (which might force selfing in the absence of such pollen – the reproductive assurance hypothesis, Lloyd, 1979) but to variation in population structure. Depending on the trend of changes in population structure, an increase or a decrease of selfing rates is expected. Indeed such opposite evolutionary trends within a same genus colonizing a new habitat have been observed (Delph, 1990).

Our results suggest that to characterize reproductive systems, it is most important to discriminate inbreeding due to selfing from biparental inbreeding. In view of the present results, analysing population structure simply in terms of a 'selfing equivalent' (i.e. by simply measuring the inbreeding coefficient within populations) could lead to erroneous conclusions about the selective mechanisms acting within populations. Measures of the proportion of inbreeding due to consanguineous matings between relatives, such as proposed by Ritland (1986), are instrumental in allowing the discrimination of biparental inbreeding and selfing (see also Ritland, 1984 and Brown *et al.* 1990). Additionally, knowledge concerning the reproductive units and their effective population size is essential to determine the scale at which selection acts. Indirect evidence in favour of significant population structure is the variation of fitness of progeny depending on the distance between parents: if the products of self-fertilization or crosses among sibs have reduced viability relative to outcrossed progeny, progeny from neighbouring plants in natural populations are expected to have a lower fitness than those from distant plants, if relatedness declines with distance. In model [3] and with *Fdisp = Mdisp = 1* and *L* = 48, the inbreeding depression measured within the neighbourhood was approximately halved (0·27 s.d. = 0·01) compared to that measured when the parents were randomly chosen in the same population (0·63 s.d. = 0·03). Such proximity dependent crossing success has been demonstrated in several species (see review in Waser, 1993), and suggests that mating events within the neighbourhood are often between fairly close relatives, but also that, despite the high likelihood of mating between relatives, considerable genetic load is maintained even in inbred individuals.

4.6. *Inbreeding depression and the inbreeding history of populations*

The model presented here shows that local mating can result in a positive relationship between inbreeding depression and the inbreeding coefficient, at both within and between species level. In other words, the purging process is not the rule in our model. Although there is considerable evidence of such a purging process in the case of selfed lines of cultivated species (Wright, 1977), it raises the question about the general occurrence of the purging process in natural populations. Based upon the available data, the relationship between the selfing rate and inbreeding depression remains unclear: comparisons of cultivated species indicate that inbreeding depression may occur in regular selfers but that it is usually less severe than in regular outbreeders, although in natural populations inbreeding depression shows no obvious relationship with the outcrossing rate (Charlesworth & Charlesworth, 1987). In most of these studies, the extent of biparental inbreeding is not known. To test for the influence of restricted gene flow and population structure on the evolution of the selfing rate, data on the covariation of inbreeding depression and the inbreeding coefficient in natural populations across several species are needed. A recent comparison proposed by Waller (1993) showed that the correlation coefficient between inbreeding depression and the inbreeding level in natural populations does not always support the purging process: while in *Mimulus guttatus* (Waller, 1984; Knight & Waller, 1987) a negative relationship occurs (as expected from the purging process hypothesis), a positive one is observed in *Impatiens capensis* (Ritland, 1990). On the other hand, if the purging process works, one can expect a positive correlation between population size and the level of inbreeding depression assuming that populations have previously experienced inbreeding during several generations, and that population size does not vary too fast. This is not necessarily the case: for example *Scabiosa columbaria* populations show significant inbreeding depression despite their small size (Van Treuren *et al.* 1994).

5. Conclusion

The overall conclusion from our study is that a stable population subdivision might favour mixed mating systems. Compared to single unstructured populations, where selfing is almost always selected, this corresponds to selection in favour of outcrossing. Other ecological or genetic factors have been proposed to explain mixed mating systems: overdominance at loci determining fitness (Campbell, 1986; Charlesworth & Charlesworth, 1987), sex asymmetry (model in which resource allocation to male and female function is variable between indi-

viduals (Charlesworth & Charlesworth, 1978, 1981; Gregorius, 1982), or pollen discounting (Lloyd, 1979; Holsinger, 1991), local adaptation (Schoen & Lloyd, 1984; Holsinger, 1986; Campbell & Waser, 1987), inbreeding depression following a decreasing exponential function in consecutive generations of selfing (Maynard Smith, 1977; Damgaard *et al.*, 1992). In the model presented here, due to a reversal of the purging process, the selected mating system is a stable equilibrium which confirms the verbal model proposed by Waller (1993), that population structure parameters (limited gene flow and small population size) can affect the purging process and thus modify the outcome of selection on mating systems. In contrast, the conditions required by Uyenoyama's (1986) model for the selection of mixed mating systems under biparental inbreeding are not met in our model, and the mechanism by which intermediate selfing rate are maintained is not the same.

Further empirical studies of the relationship between population structure and factors affecting the evolution of the mating system (such as inbreeding depression and reproductive success) are required to test the precise role of population structure in the maintenance of evolutionary stable mixed mating systems.

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Appendix

Sinusoidal function used to determine the recruitment probability in the model [3*]

For an individual (I) which position on the grid is determined by its coordinates (x, y), the area value is calculated as:

$$area(I) = f(x, y) = a + \frac{\sin(2\pi k x') \times \sin(2\pi k y')}{b}$$

where $x' = 1 - x/L$ and $y' = 1 - y/L$. k is an integer determining the number of peaks (see figures below).

The mean of the distribution function is: $\bar{M}_{area} = \int_0^1 f(x, y)\, dx\, dy = a$, and the variance is: $f(x, y)$, with $a = 0.5$ and $b = 2.8$.

The distribution of $f(x, y)$ in the case of a 4×4 grid is given on Figs. A1 and A2.

In the two former cases, there are *spatial and temporal* correlations for $f(x, y)$ among individuals.

If *Fdisp* is large (*Fdisp* $= \infty$), the positions of a mother plant and its offspring and consequently, their *area* values (f) are no more correlated. Individuals are only *spatially* correlated for $f(x, y)$.

If *Fdisp* $= 0$ and k is large (such that there are more peaks than individuals (200)), the spatial correlation disappears and there is only a *temporal* correlation for $f(x, y)$ among individuals.
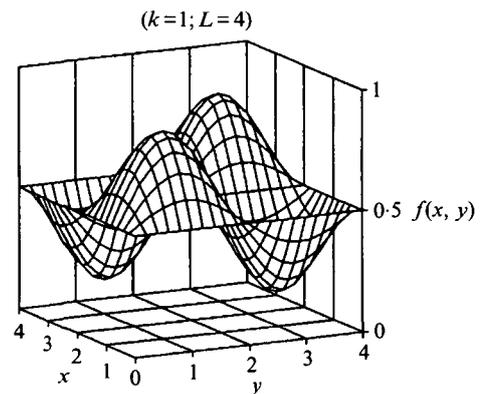
$(k = 1; L = 4)$

Fig. A1. Distribution of $f(x, y)$ in the case of a 4×4 grid ($k = 1$; $L = 4$).
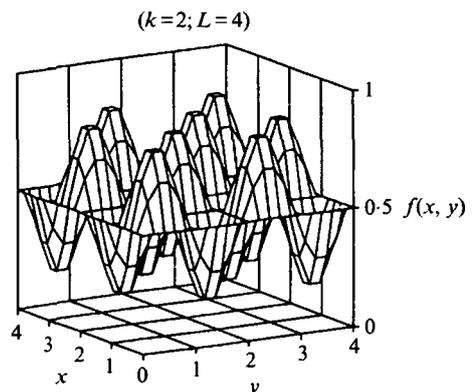
$(k = 2; L = 4)$

Fig. A2. Distribution of $f(x, y)$ in the case of a 4×4 grid ($k = 2$; $L = 4$).