

Partial selfing as an optimal mating strategy

CHRISTIAN DAMGAARD*, DENIS COUVET† & VOLKER LOESCHCKE

Department of Genetics and Ecology, University of Aarhus, Denmark †Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, Montpellier, France

For a deterministic population genetic model, we have shown that partial selfing can be an optimal mating strategy. The only necessary assumption is that inbreeding depression in consecutive generations of selfing is described by a decreasing exponential function. The model gave an estimate of the expected selfing rate in a population with mixed mating and a known inbreeding depression function. Calculations were done for both a one-locus and a co-dominant two-locus model. There were unstable or stable polymorphic equilibria that were dependent on the selfing rate of the heterozygotes. The model was shown to be in good agreement with data on inbreeding depression and selfing rates from the literature.

Keywords: ESS, inbreeding depression, mixed mating, outcrossing rate, selfing rate.

Introduction

One of the important components in the mating system of self-compatible hermaphroditic plants is the selfing rate. The evolution of selfing rates can be viewed as a conflict between 'cost of outcrossing' and inbreeding depression (Maynard Smith, 1978; Charlesworth, 1980; Feldman & Christiansen, 1984; Holsinger *et al.*, 1984). The above studies show that if the inbreeding depression (i.e. the relative difference in fitness between selfed and outcrossed individuals) is less than 0.5, and the contribution to the pollen pool is independent of the selfing rate, genotypes that self-fertilize will spread in a population, and the selfing rate of the population will increase to 1. On the other hand, if the inbreeding depression is greater than 0.5, the evolutionary stable selfing rate is 0.

Campbell (1986) and Holsinger (1988) have questioned the importance of inbreeding depression for the evolution of mating systems. They showed that the degree of linkage between a locus controlling fitness and a locus controlling the selfing rate can be of greater importance than the overall inbreeding depression. In a stochastic model, Holsinger (1988) found selection for increased selfing even though inbreeding depression was greater than 0.5.

The genetic basis of inbreeding depression is poorly understood. The available data suggest that many loci

with deleterious recessive or partly recessive alleles are maintained in populations by a mutation-selection balance and that overdominance is of less importance (Charlesworth & Charlesworth, 1987). Campbell (1986) argued that a change in the mating system will alter the inbreeding depression, and that not all individuals in a population of genetically diverse individuals will experience the same inbreeding depression. If there is a change in mating system, then the selection against the deleterious loci will change. An increase in selfing rate will decrease inbreeding depression, and favour a proportionally higher level of dominance (Lande & Schemske, 1985; Charlesworth & Charlesworth, 1987; Charlesworth *et al.*, 1990). In a partially selfing population there will be a positive association between homozygotes at different loci (Bennet & Binet, 1956), i.e. some individuals will have more homozygous loci than expected from one-locus genotype frequencies. These individuals are likely to show a higher inbreeding depression.

An individual from an outcrossing event will be more heterozygous than an individual from several generations of consecutive selfing. Inbreeding depression has been shown to be an increasing function of the inbreeding coefficient. Schuster & Michael (1976) found a decelerating decrease in yield with the number of generations of consecutive selfing in winter rape seed (*Brassica napus*), and the same trend was found in beans (*Vicia faba*) (Monti & Frusciante, 1984), alfalfa (*Medicago sativa*) (Torssell, 1929; Tysdal *et al.*, 1942),

*Correspondence.

barley (*Hordeum* ssp.) (Hagberg, 1953), rye (*Secale cereale*) (Lundquist, 1969), and maize (*Zea mays*) (e.g. Neal, 1935 and Good & Hallauer, 1977).

Whether partial selfing is an evolutionary stable strategy in some populations or only a transition phase, is currently under debate. Lande & Schemske (1985) showed, in a mutation-selection model, that a small amount of selfing will cause a decrease in the inbreeding depression. This result was confirmed by Charlesworth *et al.* (1990) for a multi-locus model without linkage, using a multiplicative fitness function. Kondrashov (1985) used a truncation selection model, and suggested that conditions may exist where partial selfing is an evolutionary stable strategy. Using a synergistic fitness function, Charlesworth *et al.* (1991) found that a selfing rate close to complete selfing could be an evolutionary stable strategy in some cases. Charlesworth & Charlesworth (1990) showed that populations with high levels of symmetrical overdominance can have partial selfing as an evolutionary stable mating strategy.

Lande & Schemske (1985) concluded from their results that only predominant outcrossing (maintained by high inbreeding depression and/or by some obligate outcrossing mechanism, e.g. self-incompatibility) or predominant selfing are stable mating strategies. Populations with partial selfing are therefore regarded as populations in transition from outcrossing to selfing. Schemske & Lande (1985) tested this hypothesis by plotting the frequencies of different selfing rates from the literature, and they found a bimodal distribution. The use of this bimodal distribution was criticized, however, because the data only came from a few taxa (Waller, 1986). Aide (1986) pointed out that if the data were grouped into wind-pollinated species and animal-pollinated species, only the wind-pollinated species showed a bimodal distribution, and these species originated from only two families (*Poaceae* and *Pinaceae*).

Another approach to understanding the evolution of selfing rates is to look at the ecology of pollination events at different population densities (Ziehe & Gregorius, 1988; Holsinger, 1991). That is, inbreeding depression can be ignored, and partial selfing can be shown to be an evolutionary stable strategy by considering the ratio between pollen used for selfing and pollen that is 'exported' from the flower (pollen discounting) (Holsinger, 1991).

Maynard Smith (1977, 1978) showed that differences in inbreeding depression that are dependent on the number of consecutive generations of selfing can lead to a polymorphism between a selfing allele and an outcrossing allele, or to the establishment of a genotype with partial selfing. In this paper we present the optimal selfing rate given data on inbreeding depression. We

assume that fitness, as affected by inbreeding depression, is an exponentially decreasing function of the number of consecutive generations of selfing, and that inbreeding depression is otherwise constant over time. The optimal mating strategy for a genetically unstructured population is analysed in a deterministic genetic model, and is tested using available data on inbreeding depression and selfing rates.

The model

If inbreeding depression is caused by many loci, each contributing a slightly deleterious effect to the inbred individuals, then the individual fitness is a function of the number of heterozygous loci. This is true for recessive deleterious loci and loci with symmetrical overdominance (Campbell, 1986). Since the number of heterozygous loci is halved for every consecutive generation of selfing, one would expect the immediate fitness of a family line (made by single seed descent) to approximate a decreasing exponential function of the number of consecutive generations of selfing. In a mixed mating system, there will be strong selection against highly deleterious or lethal recessive alleles in homozygotes (Lande & Schemske, 1985). This means that the genetic load in the population is not very large, and that in most cases a family line will not die out, but reach a level of constant inbreeding depression when most of the loci are in the homozygotic state.

If V_n represents the average fitness of individual plant after n generations of consecutive selfing, k is the fitness of a genotype homozygous at all loci ($0 < k < 1$), c is a shape parameter of the exponential function ($c > 0$), and V_0 is set to 1 then:

$$V_n = (1 - k) \exp(-cn) + k. \quad (1)$$

In a population of plants that self with probability s , a zygote (Z_0) (which is the result of an outcrossing event) has the probability of $V_0 (= 1)$ of reaching reproductive age (A_0). At that stage, the ovules are either self-pollinated with frequency s and form zygotes of type Z_1 , or cross-pollinated with frequency $1 - s$ and form zygotes of type Z_0 . The selfed zygotes (Z_1) have the probability V_1 of reaching the state (A_1), and will form the selfed Z_2 with a probability of s . If any ovule is cross-pollinated, the zygote will belong to the class Z_0 (see Fig. 1).

In the following, we have assumed that the plant is a anisogamous self-compatible hermaphrodite with non-overlapping generations. The genetic consequence of these assumptions is that selfing gives the nuclear genome a twofold advantage (cost of meiosis) compared to accepting foreign pollen (Maynard Smith, 1971; Uyenoyama, 1984).

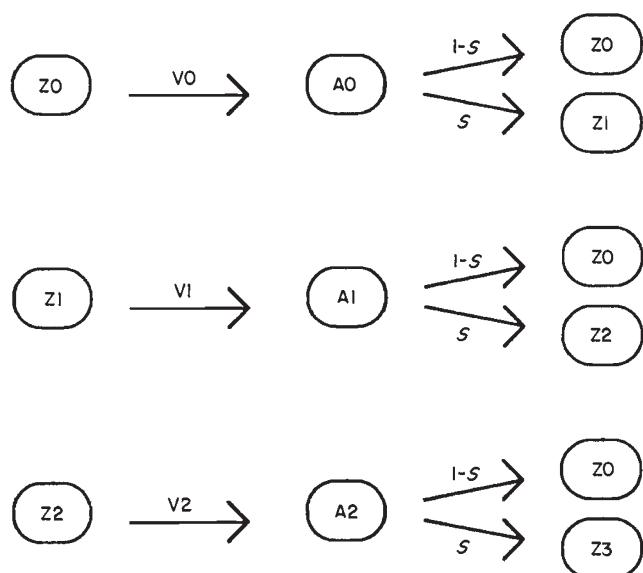


Fig. 1 Flow diagram of the different zygote classes (Z) and adult classes (A), V is the probability of reaching reproductive age, s is the selfing rate.

We further assumed that the selfing rate is controlled by one locus with many alleles, and the genotypes can have any selfing rate between 0 and 1, allowing for all combinations of dominance relationships. A deterministic computer program was written where a genotype which has been selfed n consecutive times will reach reproductive age with the probability of V_n , and then selfed with the probability of s (dependent upon the genotype) and accept foreign pollen with the probability of $1-s$. The probability of receiving pollen of a certain genotype is equal to the frequency of this genotype. If a heterozygote selfs, the offspring will be in Mendelian proportions. The fitness of the genotypes in the next generation follows the flow-pattern outlined in Fig. 1, i.e. a genotype, which has experienced n consecutive generations of selfing, has a fitness of V_n , and will leave sV_n offspring with a fitness of V_{n+1} , and $(1-s)V_n$ offspring with a fitness of 1. It is possible to follow the allele frequencies to equilibrium given the starting frequencies and selfing rates of the different genotypes.

In the following simulations we have set the maximum numbers of consecutive generations of selfing (n) to 25. The distribution of adult classes was highly skewed towards small n , even with high selfing rates and a small inbreeding depression. The results did not change when we allowed n to be higher than 25.

Results

Schuster & Michael (1976) measured inbreeding depression (decrease in yield) in winter rape seed in an

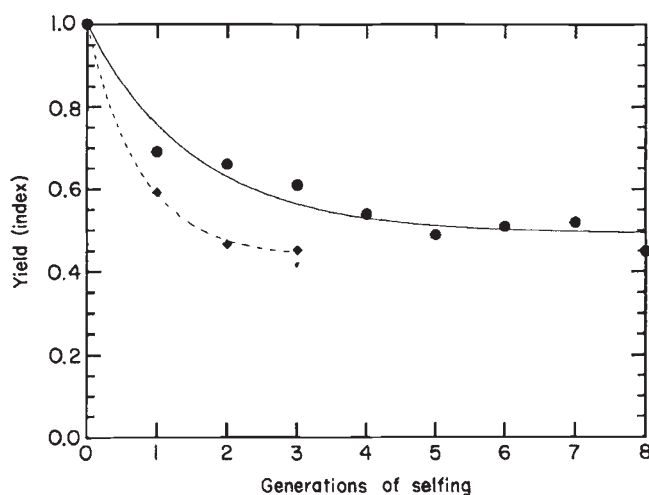


Fig. 2 Inbreeding depression data fitted by equation (1). Full line: rape seed, data from Schuster & Michael (1976). Dotted line: beans, data from Monti & Frusciante (1984).

initial population and eight consecutive generations of selfing. Their data were fitted (by least square) to the general inbreeding function as given by equation (1) with $r=0.97$ ($k=0.49$, $c=0.64$) (Fig. 2). Inbreeding depression data from three generations of selfing in beans (also measured by a decrease in yield) (Monti & Frusciante, 1984) fit equation (1) with $r=0.99$ ($k=0.44$, $c=1.30$) (Fig. 2). The fit of the other inbreeding depression data (see Introduction) all had r values above 0.95 (results not shown).

The inbreeding depression parameter values from rape seed, as calculated from the data of Schuster & Michael (1976) ($k=0.49$, $c=0.64$), are used throughout this paper as a numerical example (other parameter values gives similar results). If we start with an outcrossing population, then an allele, which has a selfing rate of 1 in homozygotes, is initially favoured, and the two alleles reach a stable equilibrium where the equilibrium frequency is dependent upon the dominance relationship. In the absence of dominance (i.e. co-dominance) there is no polymorphism. For the same c and k , and allele **a**, which in **aa** homozygotes has a selfing rate of 0.71, will be favoured over any other allele **b**, if $s(\mathbf{ab})=[s(\mathbf{aa})+s(\mathbf{bb})]/2$ (no dominance). This results is independent of the initial frequencies. We will call this selfing rate the optimal' selfing rate for the chosen c and k . Any pair of c and k will have an optimal selfing rate, defined by the selfing rate where no co-dominant allele can invade. In the following the allele with the optimal selfing rate will be called **a**.

Figure 3 gives the result of the simulation with the same c and k ($c=0.64$, $k=0.49$), for $s(\mathbf{aa})=0.71$ and $s(\mathbf{bb})=0.67$ at different initial frequencies and dominance relationships. If the allele with the optimal selfing

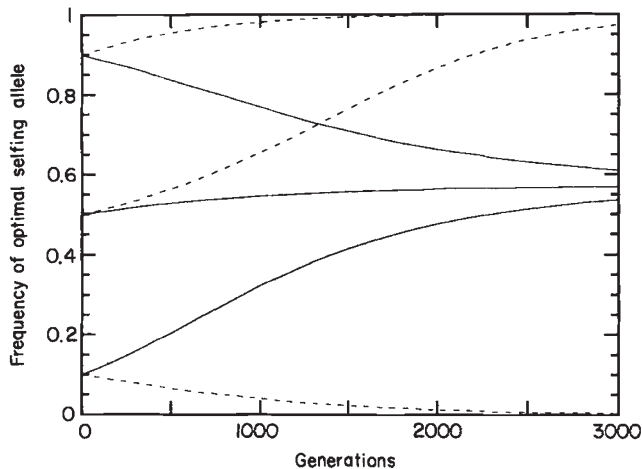


Fig. 3 Simulation with two alleles ($k = 0.49$, $c = 0.64$). The selfing rates are: $s(\mathbf{aa}) = 0.71$ and $s(\mathbf{bb}) = 0.67$, full line: $s(\mathbf{ab}) = 0.71$, dotted line: $s(\mathbf{ab}) = 0.67$, p is the frequency of \mathbf{a} .

rate is dominant, i.e. $s(\mathbf{ab}) = s(\mathbf{aa}) = 0.71$, a stable equilibrium ($p = 0.57$) exists, irrespective of the initial frequencies. If the allele with the optimal selfing rate is recessive, i.e. $s(\mathbf{ab}) = 0.67$, there is an unstable equilibrium at $p = 0.37$. If the initial frequency of \mathbf{a} is higher than 0.37, \mathbf{a} will become fixed, and if the initial frequency of \mathbf{a} is less than 0.37, \mathbf{b} will become fixed. If $s(\mathbf{bb}) = 0.75$ (i.e. higher than the optimal selfing rate) then the equilibrium properties are directly opposite. If \mathbf{a} (the optimal selfing rate) is recessive, i.e. $s(\mathbf{ab}) = 0.75$, there exists a stable equilibrium ($p = 0.73$). If \mathbf{a} is dominant the equilibrium ($p = 0.23$) is unstable.

In Fig. 4, the equilibrium properties of alleles with different selfing rates have been plotted as a function of the dominance relationship. As in Fig. 3, we have only shown the results where the alternative allele has a lower selfing rate than the optimal allele. If the allele with the optimal selfing rate is completely recessive (dominance = 0), the equilibrium is unstable. As the dominance of the optimal selfing rate increases, the frequency p , at which there is an unstable equilibrium point, decreases. At a certain level of dominance, dependent upon the selfing rate of the alternative allele, the allele with the optimal selfing rate is always fixed. At 0.5 (co-dominants) the allele with the optimal selfing rate is fixed, independent of the alternative allele and at a certain level of dominance higher than 0.5, there is a stable equilibrium when both alleles are present. The stable equilibrium is reached at lower frequencies of the optimal allele as the level of dominance increases. As the differences in selfing rates increase, i.e. $s(\mathbf{bb})$ is further from the optimal selfing rate, the range of dominance, where the allele with the optimal selfing rate is being fixed, increases as well.

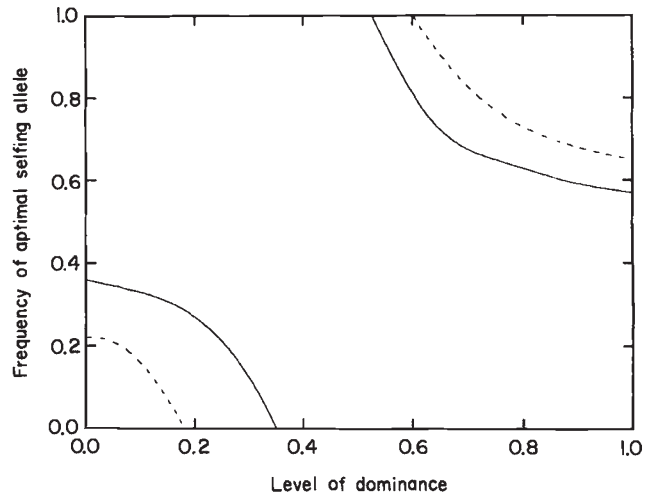


Fig. 4 The equilibrium frequencies for different levels of dominance ($k = 0.49$, $c = 0.64$). Level of dominance = 0: The allele with the optimal selfing rate is recessive [$s(\mathbf{ab}) = s(\mathbf{bb})$]. Full line: $s(\mathbf{bb}) = 0.67$, dotted line: $s(\mathbf{bb}) = 0.63$.

To analyse the equilibrium properties further, we introduced a new allele \mathbf{c} into the population where \mathbf{a} and \mathbf{b} are at a stable equilibrium. The initial increase in the new allele is highly dependent upon the selfing rate of the heterozygotes. If the heterozygotes formed with the new allele (\mathbf{ac} and \mathbf{bc}) have a higher selfing rate than the other heterozygotes, the new allele is initially favoured, even if the selfing rate of genotype \mathbf{cc} is further from the optimal selfing rate than genotype \mathbf{bb} . Depending on the selfing rate of the different genotypes, a polymorphic stable equilibrium, with either two or three alleles, may be achieved (results not shown).

Now consider a population in which there are 10 alleles with different homozygotic selfing rates, and where the first allele is dominant over the nine alleles, the second allele is dominant over the following eight alleles, etc. If the alleles are allowed to reach equilibrium, the selfing rate of the population, i.e. the selfing rate of the different genotypes times their frequencies in the population, will be equal to the optimal selfing rate (results not shown).

A co-dominant, additive, two-locus two-allele model also gives the same optimal selfing rate as the one locus model (results not shown), i.e. the genotype with the optimal selfing rate is fixed. Therefore we expect that if the selfing rate is determined by many co-dominant loci, then the optimal selfing rate found for the one-locus model will be valid for the multi-locus case.

For large c , V_1, V_2, V_3, \dots are almost equal to k . By setting $c = 10$ and $k = 0.49$ or $k = 0.51$, the model predicts $s = 0$ and $s = 1$, respectively, as the optimal selfing

rate, which is in accordance with existing theory (e.g. Maynard Smith, 1978).

By running the program with different parameter values, we found that the optimal selfing rate is an almost linear function of k , and that the slopes and intercepts of the optimal selfing rate, as a function of k , are almost linear functions of c (results not shown). This makes it possible, using linear regression, to approximate the simulation model by a simple expression of c and k , which is easy to apply to a known inbreeding depression function. The optimal selfing rate ($0 < s < 1$) is approximately:

$$s = (0.97 - 1.37c) + (-0.31 + 2.45c)k. \quad (2)$$

From this expression it is possible to construct an optimal selfing rate landscape of c and k (Fig. 5).

It is interesting, and contrary to our first expectations, that partial selfing can be an optimal mating strategy for $k > 0.5$, where inbreeding depression is always less than 0.5. From the figure, we can conclude that the optimal mating strategy is dependent not only upon the inbreeding depression measured after one generation of inbreeding, but also on the inbreeding depression in the next generations. If a 30 per cent decrease in fitness has been measured after just one generation of selfing, one would not be able to predict the optimal selfing rate. The dotted line in Fig. 5 represents the different combinations of c and k that will

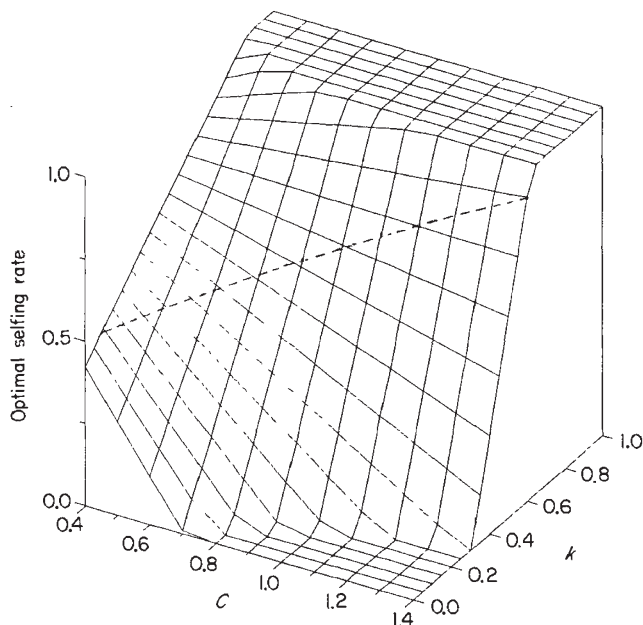


Fig. 5 The optimal selfing rates predicted by a linear approximation of the simulation model for different k and c . The dotted line represents combinations of k and c , for which V_1 is 0.7.

give a V_1 of 0.7, and the optimal selfing rates predicted from the simulation model range from 0.48 ($c=0.4$) to 0.92 ($c=1.4$). The slope of the curve suggests that populations with a high c -value (negative epistasis) are less stable at intermediary selfing rates than populations with low c -values (positive epistasis).

Discussion

If the mating system in a population is in equilibrium with the inbreeding depression, or if the change in inbreeding depression is slow compared with the evolution of the mating system, the above models predict an optimal selfing rate for the population. If a population is fixed at this selfing rate, no co-dominant allele with another selfing rate can invade the population. It is, however, possible to introduce a dominant allele with a higher selfing rate or a recessive allele with a lower selfing rate. If a population has many alleles with simple dominance relationships (see results) around the optimal selfing rate, the selfing rate of the population at equilibrium is equal to the optimal selfing rate.

For the optimal selfing rate to be an evolutionary stable strategy, two properties must be fulfilled (e.g. Christiansen, 1991): (i) if a population is fixed for the optimal selfing rate, no new allele with a different selfing rate can invade the population; and (ii) if a population is close to the optimal selfing rate, the population will converge towards the optimal selfing rate. Clearly the optimal selfing rate in the one-locus model is not an evolutionary stable strategy, since it is possible for either a recessive (or partly recessive) mutation with a lower selfing rate, or a dominant (or partly dominant) mutation with a higher selfing rate, to invade the population. However, with simple dominance relationship and many alleles the population generally is close to the optimal selfing rate.

The one-locus model allows an invasion of an allele where the selfing rate of the heterozygotes is higher than the selfing rate of the homozygotes. This seems to be a very stable situation, and increasing the selfing rate of the heterozygotes makes the polymorphism even more stable (protected) (Gregorius, 1982). It is unclear how well this situation fits a multi-locus reality, where the inter-relations of different loci (epistasis) may have a larger effect than dominance relationships within loci. Link (1990) found that bean plants (*Vicia faba*), resulting from an outcrossing event, have a higher selfing rate than an average individual. This result can be interpreted in favour of the existence of alleles that give the heterozygotes a higher selfing rate than the homozygotes.

The model offers some possibility of accounting for special ecological factors that may be of importance to the evolution of the mating system. The model can be adjusted to approximate the optimal mating strategy in a genetically structured population by correcting for biparental mating with a known degree of relatedness. This situation is presently being investigated. If an increase in selfing rate is accompanied by a sizeable reduction in the pollen available for foreign pollination, and if this reduction can be expressed as a function of s , this effect can also be included in the model.

It is possible to compare the model predictions with inbreeding depression and selfing rate data from the literature. When using data from agricultural plants, we know that outcrossing is effectively random. However, there is a risk that artificial selection and the breeding programme have changed the genetic make-up, such that the mating system is adapted to the inbreeding depression in former generations.

The inbreeding depression data from winter rape seed (Schuster & Michael, 1976) gave an optimal selfing rate of 0.71. The selfing rate in rape seed has been estimated a number of times and found to lie around 0.67 (e.g. Olsson, 1960 and Damgaard, 1990). However, Brandle & McVetty (1989) measured the inbreeding depression in summer rape seed and found a smaller maximum inbreeding depression ($1 - k$) than Schuster & Michael. These data would give a higher optimal selfing rate.

The optimal selfing rate, using inbreeding depression data from beans (Monti & Frusciante, 1984) was 0.47. In the same study, the selfing rate in the presence of pollinators was estimated to be 0.5. Monti & Frusciante (1984) reported that bean plants which had been open-pollinated twice consecutively, had a higher yield than plants that had been selfed before they were open-pollinated.

In alfalfa, inbreeding depression data from three different studies (Torssell, 1929; Tysdal *et al.*, 1942) gave optimal selfing rates of 0, 0.22 and 0.43 compared with a selfing rate in alfalfa of 0.11 (Tysdal *et al.*, 1942).

Barley, which is predominately selfing, had [in a study by Hagberg (1953)] a low inbreeding depression ($c = 0.49$, $k = 0.84$) corresponding to an optimal selfing rate of 1. Rye, which is predominately outcrossing, had a high inbreeding depression [$c = 0.88$, $k = 0.17$ (Lundquist, 1969)] corresponding to an optimal selfing rate of 0.05.

Most studies of inbreeding depression in maize, which is normally considered to be an outcrossing species, have been done with synthetic populations, i.e. crosses between inbred lines. Deleterious recessive alleles have been selected against in such populations, and are not suspected to be in equilibrium with the

mating system. The inbreeding depression data (e.g. Good & Hallauer, 1977) suggest that a genotype with partial selfing will be able to invade a synthetic corn population. Kahler *et al.*, (1984) reported that two maize populations did appear to have non-random mating and they estimated the selfing rate to be about 0.10.

In *Plantago coronopus*, inbreeding depression data from a natural population predicted an optimal selfing rate of 0.26. The same population had a selfing rate, under field conditions, between 0.10 and 0.30 (personal communication; Hans Koelewyn).

To aid comparisons with our models, we suggest that inbreeding depression data should be gathered in the following way: (i) in a population with a known selfing rate, an initial population of outcrossed individuals should be measured for characters relevant to fitness, (ii) to avoid selection against inbreeding depression, the next generations should be made by single seed descent from the former generation which has been selfed; and (iii) the selfed generations should be measured for the same fitness related characters until there is no further decrease in these characters. It is possible to obtain a good estimate of the inbreeding depression function by analysing two selfed generations and estimating the maximum inbreeding depression (e.g. by regeneration of chromosome doubled anther cultures). To account for competition effects, the different generations of consecutive selfing, weighted by their expected frequencies in a population, should be sown randomly in a plot. For more information about measuring inbreeding depression see, e.g. Lynch (1988).

To test fully the possibility that partial selfing is an evolutionary stable strategy, it is essential to achieve good estimates of the inbreeding depression from natural populations in a stable environment with a mixed mating strategy. This will make it possible to analyse whether selection against inbreeding depression is so strong that partial selfing is a transition phase as predicted by Lande & Schemske (1985) and Charlesworth *et al.* (1990).

Acknowledgement

We are grateful for helpful comments on previous drafts of the manuscript by Freddy B. Christiansen, Barbara Giles, Subodh Jain, and Robert Krebs. Part of this work was supported by Carlsbergfondet and Statens Naturvidenskabelige Forskningsfond.

References

- AIDE, T. M. 1986. The influence of wind and animal pollination on variation in outcrossing rates. *Evolution*, **40**, 434–435.

- BENNET, J. H. AND BINET, F. E. 1956. Association between Mendelian factors with mixed selfing and random mating. *Heredity*, **10**, 51–55.
- BRANDLE, J. E. AND MCVETTY, P. B. E. 1989. Effects of inbreeding and estimates of additive genetic variance within seven summer oilseed rape cultivars. *Genome*, **32**, 115–119.
- CAMPBELL, R. B. 1986. The interdependence of mating structure and inbreeding depression. *Theor. Pop. Biol.*, **30**, 232–244.
- CHARLESWORTH, B. 1980. The cost of sex in relation to mating system. *J. Theor. Biol.*, **84**, 655–671.
- CHARLESWORTH, D. AND CHARLESWORTH, B. 1987. Inbreeding depression and its evolutionary consequences. *Ann. Rev. Ecol. Syst.*, **18**, 237–268.
- CHARLESWORTH, D. AND B. CHARLESWORTH. 1990. Inbreeding depression with heterozygote advantage and its effect on selection for modifiers changing the outcrossing rate. *Evolution*, **44**, 870–888.
- CHARLESWORTH, D., MORGAN, M. T. AND CHARLESWORTH, B. 1990. Inbreeding depression, genetic load, and the evolution of outcrossing rates in a multilocus system with no linkage. *Evolution*, **44**, 1469–1489.
- CHARLESWORTH, B., MORGAN, M. T. AND CHARLESWORTH, D. 1991. Multilocus models of inbreeding depression with synergistic selection and partial self-fertilization. *Genet. Res. Camb.*, **57**, 177–194.
- CHRISTIANSEN, F. B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* **138**, 37–50.
- DAMGAARD, C. F. 1990. *Evolutionen af parringsystemer hos hermafroditiske planter — med eksempel i raps*. M. Sc. Thesis, Aarhus University.
- FELDMAN, M. V. AND CHRISTIANSEN, F. B. 1984. Population genetic theory of the cost of inbreeding. *Am. Nat.*, **123**, 642–653.
- GOOD, R. L. AND HALLAUER, A. R. 1977. Inbreeding depression in maize by selfing and full-sibbing. *Crop Sci.*, **17**, 935–940.
- GREGORIUS, H.-R. 1982. Selection in plant populations of effectively infinite size II. Protectedness of a biallelic polymorphism. *J. Theor. Biol.*, **96**, 689–705.
- HAGBERG, A. 1953. Heterosis in barley. *Hereditas*, **39**, 325–347.
- HOLSINGER, K. E., FELDMAN, M. W. AND CHRISTIANSEN, F. B. 1984. The evolution of self-fertilization in plants: A population genetic model. *Am. Nat.*, **124**, 446–453.
- HOLSINGER, K. E. 1988. Inbreeding depression doesn't matter: The genetic basis of mating-system evolution. *Evolution*, **42**, 1235–1244.
- HOLSINGER, K. E. 1991. Mass action models of plant mating systems: the evolutionary stability of mixed mating systems. *Am. Nat.*, **138**, 606–622.
- KAHLER, A. L., GARDNER, C. O. AND ALLARD, R. W. 1984. Non-random mating in experimental populations of maize. *Crop Sci.*, **24**, 350–354.
- KONDRASHOV, A. S. 1985. Deleterious mutations as an evolutionary factor. II. Facultative apomixis and selfing. *Genetics*, **111**, 635–653.
- LANDE, R. AND SCHEMSKE, D. W. 1985. The evolution of self-fertilization and inbreeding depression in plants. 1 Genetic models. *Evolution*, **39**, 24–40.
- LINK, W. 1990. Autofertility and rate of cross-fertilization: crucial characters for breeding synthetic varieties in faba beans (*Vicia faba* L.). *Theor. Appl. Genet.*, **79**, 713–717.
- LUNDQUIST, A. 1969. Some effects of continued inbreeding in an autotetraploid highbred strain of rye. *Hereditas*, **61**, 361–399.
- LYNCH, M. 1988. Design and analysis of experiments on random drift and inbreeding depression. *Genetics*, **120**, 791–807.
- MAYNARD SMITH, J. 1971. The origin and maintenance of sex. In: Williams, G. C. (ed.) *Group Selection*, Aldine-Atherton, Chicago. pp. 163–175.
- MAYNARD SMITH, J. 1977. The sex habit in plants and animals. In: Christiansen, F. B. and Fenchel, T. M. (eds) *Measuring Selection in Natural Populations*. Springer-Verlag, Berlin. pp. 315–331.
- MAYNARD SMITH, J. 1978. *The Evolution of Sex*. Cambridge University Press Cambridge. pp. 193–200.
- MONTI, L. M. AND FRUSCIANTE, L. 1984. Selection methods for yield improvement in faba beans. In: Hebblethwaite, P. D. et al. (eds) *Vicia faba: Agronomy, Physiology and Breeding*. Dr. W. Junk Publishers, The Hague.
- NEAL, N. P. 1935. The decrease in yielding capacity in advanced generations of hybrid corn. *J. Am. Soc. Agron.*, **27**, 666–670.
- OLSSON, G. 1960. Self-incompatibility and outcrossing in rape and white mustard. *Hereditas*, **46**, 241–252.
- SCHEMSKE, D. W. AND LANDE, R. 1985. The evolution of self-fertilization and inbreeding depression in plants. 2 Empirical observations. *Evolution*, **39**, 41–52.
- SCHUSTER, W. AND MICHAEL, J. 1976. Untersuchungen über Inzuchtdepression und Heterosiseffekte bei Raps (*Brassica napus oleifera*). *Z. Pflanzenzuchtung*, **77**, 56–66.
- TORSSELL, R. 1929. Självsterilitet hos luzern (*Medicago sativa* och *M. media*) *Nord. Jordbrugsforsk. Beret. Kong. i Helsingfors, Kbenhavn*. **4**, 666–669.
- TYSDAL, H. M., KISSELBACH, T. A. AND WESTOVER, H. L. 1942. *Alfalfa breeding*. Research Bulletin 124, College of Agriculture University of Nebraska, Lincoln, Nebraska.
- UYENOYAMA, M. K. 1984. On the evolution of parthenogenesis: a genetic representation of the 'cost of meiosis'. *Evolution*, **38**, 87–102.
- WALLER, D. M. 1986. Is there disruptive selection for self-fertilization? *Am. Nat.*, **128**, 421–426.
- ZIEHE, M. AND GREGORIUS, H.-R. 1988. Selection caused by self-fertilization. II. Ecological constraints on selfing advantage. *J. Evol. Biol.*, **1**, 233–253.