The Effect of Pollen Limitation on Plant Reproductive Systems and the Maintenance of Sexual Polymorphisms

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Insufficient pollination can affect the reproductive output and the rate of outcrossing of individual plants. We use a phenotypic model to explore the effect of pollen limitation on the evolution of plant reproductive systems. Compared to situations without pollen limitation, we show that conditions for the stability of different reproductive systems can change under pollen limitation: hermaphrodites are maintained under a larger set of conditions at the expense of unisexual types, especially males. We also show that trioecy, i.e., coexistence of hermaphrodites, males and females, can be evolutionarily stable, which is not the case in the absence of pollen limitation.

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In their theoretical studies of sex-ratio evolution in gynodioecious populations, Lewis (1941) and Lloyd (1974) proposed that seed production in females compared to hermaphrodites can be affected by pollen limitation. Pollen limitation can reduce the relative seed production in females compared to hermaphrodites if the hermaphrodites are self-compatible and if selfing requires the action of the pollination agent (wind or pollinator) to a lesser extent than outcrossing. In animal-pollinated species, a lack of pollinators could also alter the relative fertilities of females and hermaphrodites if hermaphrodites are more attractive to pollinators than females.

Differences in pollinator activity have also been invoked to explain changes in reproductive systems within and between species. A decrease in pollinator activity, causing an increase in the selfing rate of hermaphrodites, could favour the evolution of sexual dimorphism (gynodioecy or dioecy) to enforce outcrossing (Heine 1937 in Delph 1990). Delph (1990) found that sexual systems in species of *Hebe* tend to change from hermaphrodism to dioecy with increasing altitude and changes in the pollinator fauna. The reverse can also be argued: it could be better to be a self-compatible hermaphrodite if there is a real lack of pollinators, even if inbreeding depression is strong. *Parahebe* species from high altitudes have indeed evolved autogamy (Garnock-Jones 1976 in Delph 1990). *Armeria maritima* loses its heterostylic incompatibility system and regains self-compatibility at high latitudes (Baker 1966). Bierzychudek (1987), after studying apomictic and sexual forms of *Antennaria parvifolia*, proposed that apomixis could be an adaptation to the absence of pollinators in self-incompatible taxa.

In order to examine the effect of pollen limitation on the evolution of plant reproductive systems, we include this phenomenon in a phenotypic model of gender selection. The severity of pollen limitation can depend not only on the efficiency of the pollination agent but also on the frequency of pollen producers in a population. Lewis (1941) thus proposed that the probability that ovules of

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females will be fertilised decreases when the frequency of non-pollen producers (females) increases in a population. Lloyd (1974) used the following function for that probability: $p = 1\text{-}f^x$, where f is the frequency of females in the population and x is the average number of pollinator visits a flower receives. We hypothesise here that pollen limitation is likely to reduce the number of outcrossed ovules not only in females but also in hermaphrodites. We consider a general model where selfing may also require some pollinator visitation and where the probability that a non-selfed ovule will be fertilised can take various forms as a function of the frequency of females. The model below is simplified in that the "a priori" selfing rate is considered fixed, i.e., this selfing rate is determined by the morphology and phenology of the species. The realised selfing rate, i.e., the number of seeds produced by selfing versus the total number of seeds produced, does depend on pollination intensity.

Model and calculations

Fitnesses of the sexual phenotypes

We follow Charnov et al. (1976) and Charnov (1982) in writing the fitnesses of the different sexual phenotypes and use the following notations:

α: relative pollen production of hermaphrodites compared to males.

β: relative seed production of hermaphrodites compared to females (in the absence of pollen limitation and inbreeding depression).

s: "a priori" selfing rate of hermaphrodites, i.e., in the absence of pollen limitation (the realised selfing rate depends on the intensity of pollen limitation and is equal to: $sp_s \,/\, [sp_s + (1\text{-}s)p_c]$).

d: inbreeding depression (fitness of an offspring produced by selfing compared to an offspring produced by outcrossing = $1\text{-}d$).

p_s, p_c: probability that a flower will be visited enough to produce selfed (s) or outcrossed (c) seeds.

f, m, h: frequencies of females, males and hermaphrodites in the population.

f_G, f_D: frequencies of females in gynodioecious and dioecious populations at equilibrium.

W_f, W_m, W_h: relative fitnesses of females, males and hermaphrodites.

The fitnesses of the different sexual phenotypes are:

$$W_f = p_c,$$

$$W_h = \beta[1 - s)p_c + 2s(1-d)p_s] + \frac{\alpha[fp_c + h\beta(1-s)p_c]}{m + \alpha h},$$

$$W_m = \frac{fp_c + h\beta(1-s)p_c}{m + \alpha h}$$

We can see that only the ratio of the probabilities of receiving enough pollinator visits to outcross or to self affects the relative fertilities of the different sexual phenotypes. This ratio will be denoted p_f $(= p_c/p_s)$ in general and p_0 when the frequency of females is 0.

As the fitnesses are relative, we can divide their expressions by P_c to obtain:

$$W_f = 1,$$

$$W_h = \beta\left[1 - s + 2s\,\frac{1-d}{p_f}\right] + \frac{\alpha[f + h\beta(1-s)]}{m + \alpha h},$$

$$W_m = \frac{f + h\beta(1-s)}{m + \alpha h},$$

where the pollination factor clearly appears.

Conditions for the stability of the different reproductive systems

The three sexual phenotypes can be combined to give hermaphrodism, gynodioecy (coexistence of females and hermaphrodites), androdioecy (males and hermaphrodites), dioecy (females and males) and trioecy (females, males and hermaphrodites). We searched for conditions of stability for each of these reproductive systems by calculating the conditions under which a new sexual phenotype will increase in a population with these reproductive systems. The method is the following: 1) at equilibrium, the fitnesses of the sexual phenotypes present in the population are equal; 2) a new sexual type will increase if its fitness (when this new sexual type is rare) is greater than the fitness of the present types. The different situations are:

Population dioecious, condition for an hermaphrodite to increase

In a dioecious population at equilibrium, $W_f = W_m$, which gives $m = f = ½$ and $W_f = W_m = 1$. An hermaphrodite will thus increase if $W_h > 1$, which gives:

$$\beta\left[1 - s + 2s\,\frac{1-d}{p_{f_D}}\right] + \alpha > 1; \qquad \text{(I)}$$

i.e., dioecy is stable if $\beta\left[1 - s + 2s\,\frac{1-d}{p_{f_D}}\right] + \alpha < 1$.

Population hermaphroditic, condition for a female to increase

A female increases in a hermaphroditic population if $W_f > W_h$, which gives:

$$\beta\left[1 - s + s\,\frac{1-d}{p_0}\right] < ½. \qquad \text{(II)}$$

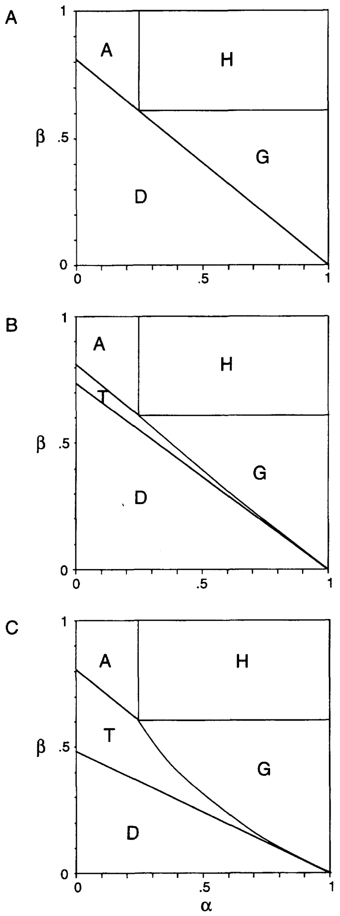

Fig. 1. Stable reproductive systems depending on the relative male (α) and female (β) fertilities of hermaphrodites, in the absence of pollen limitation (A), with a weak pollen limitation (B, $p_f = 1\text{-}f^8$) and with a strong pollen limitation (C, $p_f = 1\text{-}f$). The “a priori” selfing rate of hermaphrodites, s, is 0.6 and there is a weak inbreeding depression (d = 0.3). A: androdioecy, H: hermaphrodism, G: gynodioecy, T: trioecy, D: dioecy.

Population hermaphroditic, condition for a male to increase

$$W_m > W_h \text{ gives: } \alpha \frac{1 - s + s\dfrac{1-d}{p_0}}{1-s} < \tfrac{1}{2}. \qquad \text{(III)}$$

Population gynodioecious, condition for a male to increase

$W_f = W_h$ gives the frequency of females in a gynodioecious population as:

$$f_g = \frac{1 - 2\beta\left[1 - s + s\dfrac{1-d}{p_{f_g}}\right]}{2\left[1 - \beta\left[1 - s + s\dfrac{1-d}{p_{f_g}}\right]\right]}.$$

$$W_m > W_h \text{ then gives: } \alpha + \beta\left[1 - s + 2s\frac{1-d}{p_{f_g}}\right] < 1. \qquad \text{(IV)}$$

Population androdioecious, condition for a female to increase

$$W_h = W_m \text{ gives: } m = \frac{(1-s) - 2\alpha\left[1 - s + s\dfrac{1-d}{p_0}\right]}{2(1-\alpha)\left[1 - s + s\dfrac{1-d}{p_0}\right]}.$$

$$W_f > W_m \text{ gives: } \alpha + \beta\left[1 - s + 2s\frac{1-d}{p_0}\right] < 1. \qquad \text{(V)}$$

In order to have a stable trioecious reproductive system, each of the three sexual phenotypes must increase when rare. This is obtained when: a) hermaphrodites increase in a dioecious population, females increase in a hermaphroditic population and males increase in a gynodioecious population; i.e., when (I), (II) and (IV) are true, or b) hermaphrodites increase in a dioecious population, males increase in a hermaphroditic population and females increase in an androdioecious population, i.e., when (I), (III) and (V) are true.

In a trioecious reproductive system at equilibrium, $W_f = W_m = W_h$. Frequencies of the different sexual phenotypes are thus given by the following systems of equations:

$$\left\{\begin{array}{l} f + h\beta(1-s) = \alpha h + m \\ \beta\left[1 - s + 2s\dfrac{1-d}{p_f}\right] + \alpha = 1 \\ f + h + m = 1 \end{array}\right. \qquad \text{or,}$$

$$\left\{\begin{array}{l} \beta[1 - s + 2s(1-d)/p_f] + \alpha = 1 \\ 2f + h[\beta(1-s) + 1 - \alpha] = 1 \\ f + h + m = 1 \end{array}\right. \qquad \text{(VI)}$$

In the absence of pollen limitation (i.e., p_f = 1), the system is:

$$\left\{\begin{array}{l} \beta[1 + s(1-2d)] + \alpha = 1 \\ f + h\beta(1-sd) = \tfrac{1}{2} \\ f + h + m = 1 \end{array}\right. \qquad \text{(VII)}$$

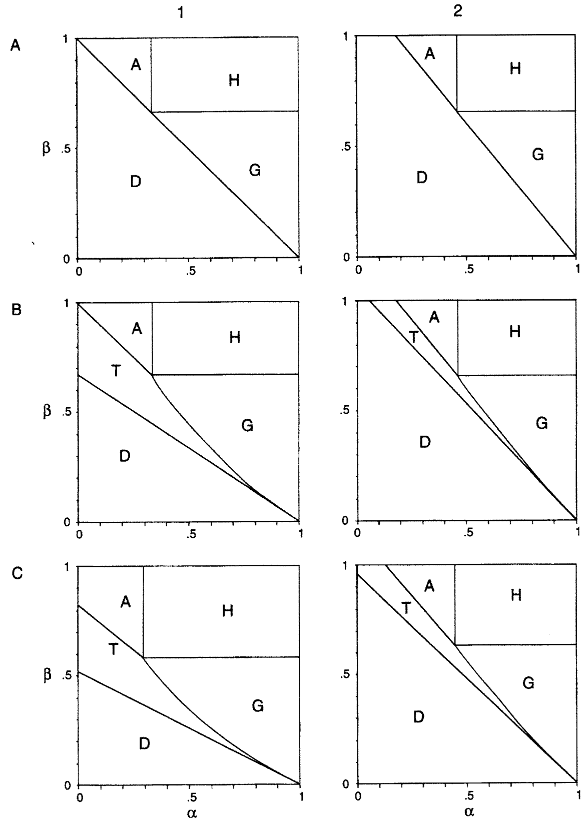

Fig. 2. Stable reproductive systems depending on the relative male (α) and female (β) fertilities of hermaphrodites, in the absence of pollen limitation (A), with pollen limitation in the presence of females only (B, $p_f = 1\text{-}f$), with pollen limitation even in the absence of females (C, $p_f = 0.7(1\text{-}f)$). In case 1, the "a priori" selfing rate of hermaphrodites, s, is 0.5 and the inbreeding depression, d, is 0.5. In case 2, $s = 0.3$ and $d = 0.8$. A: androdioecy, H: hermaphrodism, G: gynodioecy, T: trioecy, D: dioecy.

Examples

We have considered two kinds of functions to express pollen limitation:

1. The function proposed by Lloyd (1974), $p_f = 1\text{-}f^x$. In our model, this function implies that in the absence of females, selfing is as limited by pollinator activity as outcrossing. Examples of stable reproductive systems obtained under strong pollen limitation ($x = 1$), under weak pollen limitation ($x = 3$) and in absence of pollen limitation are illustrated on Fig. 1.

2. Because it is likely that outcrossing needs more pollinator visits than selfing, even in the absence of females, we also use the function $p_f = a\ (1\text{-}f^x)$, with $a < 1$ (Fig. 2).

Simplifications of the conditions above for these functions of pollen limitation are given in the Appendix. Examples of sex-ratios are given in Table 1.

Results and discussion

Changes in reproductive systems

Our calculations indicate that pollen limitation increases the range of conditions under which hermaphrodites are present in a population, even when inbreeding depression is strong (Fig. 1, 2, Table 1). This result will hold for any function of pollen limitation, as soon as outcrossing in more limited than selfing by the availability of pollen (i.e., $p_f < 1$, see the expressions for the relative fitnesses of the sexual types). The effect of pollen limitation increases when the "a priori" selfing rate of hermaphrodites increases and when the inbreeding depression decreases (see the expressions for the fitnesses and Fig. 2). The presence of hermaphrodites can lead to the coexistence of the three sexual phenotypes (see details below) or to the displacement of males (Fig. 1 and 2, panels B and C show an increase of the gynodioecy area at the expense of dioecy; Fig. 2, panels C show an increase of the hermaphrodism area at the expense of androdioecy and dioecy) and/or females (Fig. 2, panels C show an increase of the hermaphrodism area at the expense of gynodioecy and dioecy). When outcrossing and selfing are similarly pollen limited in the absence of females ($p_f = 1\text{-}f^x$, panels B and C of Fig. 1 and panel B of Fig. 2), conditions for the increase of a rare female strategy are obviously similar to those in the absence of pollen limitation. The areas of stability of hermaphrodism and androdioecy thus remain unchanged. When pollinators visitation is more limiting for outcrossing than for selfing even in the absence of females ($p_f = a\ (1\text{-}f^x)$, panel C of Fig. 2), then all areas of stability of the different reproductive systems are modified. In both cases, for a given set of parameters (a priori relative fertilities, a priori selfing rate, inbreeding depression), the stable reproductive system can change from dioecy to trioecy, and from trioecy to gynodioecy as pollination becomes more limiting (Fig. 1 and 2, Table 1).

The main effect of pollen limitation is to reduce the realised reproduction of unisexuals compared to hermaphrodites. The realised selfing rate of hermaphrodites is of course increased as some ovules fail to be outcrossed, but the difference between the realised selfing rate with (sa) and without (s) pollen limitation is usually not very large (Table 1). The selfing rate of hermaphrodites would be higher if ovules that failed to be outcrossed were then selfed. This hypothesis is not included in the calculations presented here. One can nevertheless affirm that, under this hypothesis, hermaphrodites would be even more favoured by pollen limitation. Results would thus not be qualitatively changed.

Maintenance of sexual polymorphism

Our calculations show that, for a subset of parameters, the three sexual phenotypes coexist in a population, i.e. trioecy is stable. In the absence of pollination limitation,

Table 1. Examples of stable reproductive systems and sex-ratios (frequencies of females (*f*), hermaphrodites (*h*) and males (*m*)) for different values of the selfing rate of hermaphrodites (*s*), the inbreeding depression (*d*), the function for pollen limitation and the relative male (α) and female (β) fertilities of hermaphrodites. The selfing rate achieved, $sa = s / (s + (1\text{-}s)p_f))$, has been calculated.

selfing rates		inbreeding depression	relative fertilities of hermaphrodites		pollen limitation	frequencies of sexual phenotypes			reproductive system
s	sa	d	α	β	p_f	f	h	m	
0.6	0.6	0.3	0.40	0.35	none	0.50	0	0.50	dioecy
	0.70				$1\text{-}f$	0.36	0.38	0.26	trioecy
	0.6		0.45	0.40	none	0.50	0	0.50	dioecy
	0.65				$1\text{-}f$	0.20	0.80	0	gynodioecy
	0.6		0.55	0.55	none	0.09	0.91	0	gynodioecy
	0.68				$0.7(1\text{-}f)$	0	1	0	hermaphrodism
0.5	0.5	0.5	0.50	0.40	none	0.50	0	0.50	dioecy
	0.60				$1\text{-}f$	0.33	0.48	0.19	trioecy
	0.64				$0.7(1\text{-}f)$	0.20	0.80	0	gynodioecy
0.3	0.3	0.8	0.50	0.55	none	0.50	0	0.50	dioecy
	0.43				$1\text{-}f$	0.42	0.17	0.41	trioecy

with or without selfing, the three sexual phenotypes will have equal fitnesses only if the relative fertilities of hermaphrodites compared to unisexuals are exactly on the line $\alpha+\beta(1\text{-}s\,(1-2d)) = 1$ (eq. VII), as already stated by Charnov et al. (1976) in the absence of selfing. For a given pair (α,β) on that line, the frequencies of the sexual phenotypes cannot be completely solved and a line of solution for the frequencies does exist (eq. VII). This explains why trioecy is not stable, even if the pair (α,β) meets the requirement, which is already improbable. Should the frequencies of sexual phenotypes be altered by drift or migration, selection will tend to bring them back to the line of equilibrium but not exactly at the same point. One sexual type (*f*, *m* or *h*) or the two unisexuals will eventually be lost. It can also be noted that a new sexual phenotype arriving in a population at equilibrium for the two other sexual phenotypes is at most (i.e., if the population is infinite) neutral and thus can increase only by chance.

In the case of pollen limitation and if the level of pollen limitation depends on the frequency of females, the three sexual phenotypes can have equal fitnesses for more than a line of (α,β) parameters. The conditions in (α,β) are linked to the frequencies of sexual phenotypes (eq. VI). For a given (α,β) in that set of solutions, trioecy is stable and the sexual frequencies are exactly determined.

Conclusions

Classical models of the evolution of reproductive systems show that, in the presence of inbreeding depression, an increase in the selfing rate of hermaphrodites favours the evolution of dioecy (Charlesworth and Charlesworth 1978). We show here that although a decrease in the abundance or efficiency of pollination agent increases the relative selfing rate of hermaphrodites, it does not favour the evolution of unisexuality. This is because reduced pollination affects the fitness of unisexual individuals even more strongly than it affects hermaphrodites. This situation supports Darwin (1877), who wrote: "As we must assume that cross-fertilisation was assured before an hermaphrodite could be changed into a dioecious plant, we may conclude that the conversion has not been effected for the sake of gaining the great benefits which follow from cross-fertilisation.". Rather than favouring the evolution of dioecy from hermaphrodism, reduced pollination could be responsible for evolution in the reverse direction: from dioecy to gynodioecy, androdioecy or hermaphrodism if the bisexual types reappear by mutation or migration. This has been proposed as an explanation for the androdioecious system of *Datisca glomerata* (Liston et al. 1990).

Dioecy has been said to occur more frequently in species pollinated by small, unspecialised insects (Bawa 1980, Givnish 1982). The evolutionary factor proposed is that these pollinators stay a long time on the same individual, causing high rates of selfing in hermaphrodites. We would like to emphasise that this argument can only be valid if the behaviour of pollinators is such that it reduces the outcrossing rate of hermaphrodites more than it reduces the reproduction of unisexuals. One can even say "much more" because in this "reverse hypothesis", ovules of hermaphrodites are selfed if they are not outcrossed whereas in our model, ovules of hermaphrodites are lost if they are not outcrossed.

Our model indicates that pollen limitation can be responsible for the coexistence of more than two sexual phenotypes in a population, either as an intermediate stage or as an equilibrium if the lack of pollen increases with the frequency of females in the population. Few cases of true trioecy, with separate female, male and hermaphrodite individuals, have been described. One example is the bat-pollinated columnar cactus *Pachycereus pringlei* which possesses gynodioecious and trioecious populations in the Sonoran Desert of Mexico. In this species, pollination has been shown to limit seed set in females but not in hermaphrodites and the presence of males in populations is correlated with proximity to major bat roosts (Fleming *et al.* 1994). Pollen limitation thus appears to be a major factor in the evolution of the geographically variable breeding system of this species.

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Appendix

Conditions for the stability of the different reproductive systems, for two kinds of pollen limitation, p_f.

1. $p_f = 1\text{-}f^x$

Pollen limitation does not change the frequency of females ($^1/_2$) in dioecious populations.
Conditions become:

$$\text{(I) } \beta\left[1-s+2s\frac{1-d}{1-\tfrac{1}{2}^x}\right]+\alpha>1$$

$$\text{(II) } \beta[1-sd]<\tfrac{1}{2}$$

$$\text{(III) } \alpha\,\frac{1-sd}{1-s}<\tfrac{1}{2}$$

$$\text{(IV) } \alpha+\beta\left[1-s+2s\,\frac{1-d}{1-f_G^x}\right]<1$$

$$\text{(V) } \alpha+\beta[1-sd]<1$$

The frequency of females in a gynodioecious population is given by:

$$f_G^{x+1}[-2(1-\beta(1-s))]+f_G^x[1-2(1-s)]+f_G[2(1-\beta(1-sd))]+2\beta(1-sd)-1=0.$$

If $x = 1$, then $f_G = \dfrac{1-2\beta(1-sd)}{2[1-\beta(1-s)]}$.

For $x = 3$, calculations of f_G and condition (IV) have been made using Mathematica (Wolfram Co).

2. $p_f = \text{a}\ (1\text{-}f^x)$, with $\text{a} < 1$

We have made calculations only for $x = 1$.
The frequency of females in gynodioecious populations is:

$$f_G=\frac{1-2\beta\left[1-s+s\,\dfrac{1-d}{\alpha}\right]}{2[1-\beta(1-s)]}$$

and $p_0 = a$, $p_{f_D} = \tfrac{1}{2}\,a$, $p_{f_G} = a(1-f_G)$.