

MAINTENANCE OF MALE STERILITY IN PLANT POPULATIONS

III. MIXED SELFING AND RANDOM MATING

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SUMMARY

Two models of monogenic recessive male sterility are presented, first where the male-steriles are always fully pollinated (full-fitness model) and second where they are only pollinated to the extent that hermaphrodites are crossed (limited-fitness model). Male-steriles in both models may be maintained by overdominance at the sex-control locus or by having greater ovule or seed fertility than hermaphrodites. For both models fitness of male-steriles is frequency dependent under random mating or under mixed selfing and random mating, and for the case when male-steriles are maintained only by increased fertility, expressions are derived for their equilibrium proportions and those of both hermaphrodite genotypes. Also for this latter case, fitness of male-steriles in equilibrium populations equals that of the hermaphrodites. In the full-fitness model the degree of selfing among hermaphrodites has little effect on equilibrium proportions of male-steriles, which may decline slowly, increase slowly, or remain constant with increased selfing. Except under random mating, equilibrium proportions of male-steriles are lower in the limited-fitness model and decline with increased selfing among hermaphrodites. Outcrossing rates for pollen of hermaphrodites are derived.

1. INTRODUCTION

GYNODIOECIOUS populations contain separate male-sterile and hermaphrodite individuals, and gynodioecy has been interpreted as an outbreeding mechanism. Theoretical studies of the maintenance of the male-sterile form among the hermaphrodites have been made by several authors. Lewis (1941), Ross and Shaw (1971) and Lloyd (1974*a*) showed that male-steriles could be maintained by a more than doubled seed fertility compared to hermaphrodites, while Jain (1961), Ho and Ross (1973), Valdeyron, Dommée and Valdeyron (1973) and Lloyd (1975) showed that heterozygote advantage either associated with the sex-control loci, or in the form of a general heterosis, could also result in the maintenance of male-steriles. Ross and Shaw (1971) noted that fitness values of male-steriles in gynodioecious populations were frequency dependent, while Lloyd (1974*b*) showed that genetic contributions of male-steriles and hermaphrodites may be equal at equilibrium.

The studies of Ross and Shaw (1971) and Ho and Ross (1973) assumed random mating, and one aim of the present study is to consider the effects of selfing among hermaphrodites. In addition, we derive expressions for the fitness of the male-steriles and for their equilibrium proportions.

2. FITNESS AND EQUILIBRIUM PROPORTIONS OF MALE-STERILES

We first consider a simple fitness model which applies to any mode of nuclear inheritance of male-sterility, where there is no selection. Since hermaphrodites leave descendants through both ovules and pollen, while male-steriles leave descendants through the female line only, a new male-sterile mutant, differing from hermaphrodites only in its male sterility, will suffer a considerable disadvantage. Such a mutant would be lost in the absence of some mechanism for its maintenance. When considering populations containing male-steriles and hermaphrodites it is useful to consider the offspring through the female line separately from those through the male line. When assigning fitness values, offspring of selfings and of inter-hermaphrodite crosses are thus counted twice as offspring of hermaphrodites, once in each line, while offspring of crosses between male-steriles and hermaphrodites are counted once as offspring of male-steriles, and once as offspring of hermaphrodites.

If male-steriles (in proportion f) are fully pollinated by hermaphrodites (in proportion h), we have the following scheme:

Number of offspring of male-steriles is proportional to f
 Number of offspring of hermaphrodites is proportional to $(2h + f)$.

Setting the fitness, or offspring per individual, of the hermaphrodites to 1, we have:

$$\text{Fitness of male-steriles} = h/(2h + f).$$

Since there is no selection, apart from that imposed by the male sterility itself, we may regard the above as intrinsic to populations containing both sex forms. Fitness of the male-steriles is frequency dependent, and as f becomes small, approaches an upper limit of 0.5. This result is consonant with that of Lewis (1941), who found that monogenically inherited male-steriles were only maintained in the population if their seed fertility was more than doubled. The result also agrees with the suggestion of Ross and Shaw (1971) that this requirement for a more than doubled seed fertility was probably independent of the mode of nuclear inheritance of the male sterility.

We now consider the case where male sterility is inherited through a single recessive, ms , such that genotype $ms\ ms$ (frequency f) is male-sterile, while genotypes $Ms\ Ms$ (frequency h_1) and $Ms\ ms$ (frequency h_2) are hermaphrodite. The gametic outputs of the genotypes, first as female, then as male, are w_1, w_1 for $Ms\ Ms$, 1, 1 for $Ms\ ms$ and $w_2, 0$ for $ms\ ms$. Thus we consider two mechanisms for maintenance of gynodioecy, namely that where male-steriles may be maintained by overdominance at the sex-control locus ($w_1 < 1$), and that where male-steriles are favoured because they produce more or better seed than hermaphrodites ($w_2 > 1$).

(i) *Full-fitness model*

Two mating systems will be considered. In the first, or *full-fitness* model, all ovules on male-steriles are fertilised. On hermaphrodites, a proportion s_1 of ovules are self pollinated and a proportion $t_1 = 1 - s_1$ are cross pollinated. The frequencies of seed set on the three genotypes $Ms\ Ms$, $Ms\ ms$, $ms\ ms$

are w_1h_1/D_o , h_2/D_o , w_2f/D_o respectively. The pollen pool for cross pollination has the gametic types Ms , ms with frequencies $(w_1h_1 + h_2/2)/D_p$, $(h_2/2D_p)$ respectively. In these expressions, $D_o = w_1h_1 + h_2 + w_2f$ and $D_p = w_1h_1 + h_2$ are normalising factors. The $Ms Ms$ individuals produce seed of genotype $Ms Ms$ with probability $s_1 + t_1(w_1h_1 + h_2/2)/D_p$ and seed of genotype $Ms ms$ with probability $t_1h_2/2D_p$. Similar arguments for the other two genotypes lead to the following transition equations, where h'_1 , h'_2 and f' are the new genotypic frequencies:

$$\begin{aligned} h'_1 &= s_1(w_1h_1 + h_2/4)/D_o + t_1(w_1h_1 + h_2/2)^2/D_oD_p \\ h'_2 &= s_1(h_2/2)/D_o + (t_1h_2 + w_2f)(w_1h_1 + h_2/2)/D_oD_p \\ f' &= s_1(h_2/4)/D_o + h_2(t_1h_2/2 + w_2f)/2D_oD_p. \end{aligned}$$

It can be seen immediately that $f \leq h_2$ in all generations so that the maximum frequency of male-steriles is 0.5, and this is only approached as w_2 becomes very large. It is also evident that the absence of either heterozygous hermaphrodites or male-steriles implies the absence of the other while the presence of either implies the presence of all three genotypes.

The composition of the equilibrium population is found by setting $\dot{h}_1 = h_1 = h'_1$, $\dot{h}_2 = h_2 = h'_2$, $\dot{f} = f = f'$. There will always be the trivial solution $h_1 = 1$, $h_2 = f = 0$, and certain favourable values of the parameters will give non-trivial solutions. Generally these will have to be found numerically, although in the special case of $w_1 = 1$, analytic solutions are available. In this case of equal selection for homozygous and heterozygous hermaphrodites:

$$f = \begin{cases} (w_2 - 2)/[2(w_2 - 1)] & \text{for all } t_1, \text{ if } w_2 > 2 \\ 0 & \text{if } w_2 \leq 2. \end{cases}$$

For the non-trivial case

$$h_2 = \begin{cases} w_2(w_2 - 2)/[(2w_2 - 3)(w_2 - 1)] & \text{if } t_1 = 0 \\ w_2[(t_1 + 3 - 2w_2) + Q]/[4t_1(w_2 - 1)] & \text{if } t_1 \neq 0 \end{cases}$$

and

$$h_1 = \begin{cases} w_2/[2(2w_2 - 3)(w_2 - 1)] & \text{if } t_1 = 0 \\ w_2[(t_1 - 3 + 2w_2) - Q]/[4t_1(w_2 - 1)] & \text{if } t_1 \neq 0 \end{cases}$$

where $Q^2 = (t_1 + 3 - 2w_2)^2 + 8t_1(w_2 - 2)$.

We now consider the genetic contributions made to each offspring generation by the various genotypes.

Pollen from hermaphrodites contribute to all (D_o) seed set, while ovules of hermaphrodites contribute only to (D_p) seed set on hermaphrodites. The genetic contribution of hermaphrodites through ovules relative to their total contributions is thus $w_{hf} = D_p/(D_o + D_p)$. As long as $f > 0$, $D_p < D_o$ and this relative contribution is less than 0.5. Lloyd (1974a) has emphasised that genetic contributions through pollen and ovules of hermaphrodites are not equal in gynodioecious populations.

The genetic contributions from the three genotypes are w_1h_1/D_o (ovules) + w_1h_1/D_p (pollen) for $Ms Ms$, h_2/D_o (ovules) + h_2/D_p (pollen) for $Ms ms$ and w_2f/D_o (ovules) for $ms ms$. Dividing these three contributions by corresponding genotypic frequencies (providing they are not zero) and setting the contribution (*i.e.* the fitness) of heterozygous hermaphrodites equal to 1, we find that the fitness of homozygous hermaphrodites is w_1 and that of male-steriles is $w_f = w_2D_p/(D_o + D_p)$. This latter value is w_2

times as great as w_{hj} , the genetic contribution of hermaphrodites via ovules. When $w_1 = 1$ and there is no overdominance, the fitness of male-steriles may be written as $w_j = w_2(1-f)/[2+(w_2-2)f]$ which is also equal to 1 at non-trivial equilibria. Note that in this case the genetic contribution of hermaphrodites via ovules in equilibrium populations is $\hat{w}_{hj} = 1/w_2$. For trivial equilibria we will define $\hat{w}_j = 0$. Male-steriles and hermaphrodites also produce equal genetic contributions under monogenic dominant gynodioecy (Lloyd, 1974*b*; Ross, in preparation).

In gynodioecious populations, pollen and ovules of hermaphrodites do not take part in crossing and selfing to the same extent. A proportion t_1 of ovules of hermaphrodites are cross fertilised while a proportion t_2 of pollen takes part in crossing. This proportion t_2 is necessarily the proportion of all offspring produced by crossing so that $t_2 = (t_1 D_p + w_2 f)/D_o$ and $s_2 = 1 - t_2 = s_1 D_p/D_o$. For $f > 0$ then, $s_2 < s_1$.

(ii) *Limited-fitness model*

In the second, or *limited-fitness* model, a proportion t_1 of ovules on all plants are cross pollinated regardless of genotype, so that t_1 is different from that in the full-fitness model. None of the ovules on male-steriles, but a proportion $s_1 = 1 - t_1$ of the ovules on hermaphrodites are self pollinated. Reduced cross pollination thus reduces the seed set on male-steriles.

With frequencies h_1, h_2, f as before, the frequencies of seed set are $w_1 h_1/D_o, h_2/D_o, t_1 w_2 f/D_o$ for *Ms Ms, Ms ms, ms ms* respectively, where D_o is now given by $w_1 h_1 + h_2 + t_1 w_2 f$. The pollen gametic frequencies are as in the full-fitness model and the genotype transition equations are now:

$$\begin{aligned} h'_1 &= s_1(w_1 h_1 + h_2/4)/D_o + t_1(w_1 h_1 + h_2/2)^2/D_o D_p \\ h'_2 &= s_1(h_2/2)/D_o + t_1(w_1 h_1 + h_2/2)(h_2 + w_2 f)/D_o D_p \\ f' &= s_1(h_2/4)/D_o + t_1(h_2/2)(h_2/2 + w_2 f)/D_o D_p. \end{aligned}$$

Again $f \leq h_2$ and either both or neither of f and h_2 are zero.

Non-trivial equilibria are still generally found numerically, but there are two special cases. In the case $w_1 = 1$ and $t_1 \neq 0$ the equilibrium solutions are:

$$\begin{aligned} f &= (t_1 w_2 - 2)/2(t_1 w_2 - 1) & \text{if } w_2 > 2/t_1 \\ &= 0 & \text{if } w_2 \leq 2/t_1 \end{aligned}$$

and in the non-trivial case:

$$\begin{aligned} h_2 &= w_2[(t_1 + 3 - 2t_1 w_2) + R]/[4(t_1 w_2 - 1)] \\ h_1 &= w_2[(t_1 - 3 + 2t_1 w_2) - R]/[4(t_1 w_2 - 1)] \\ \text{where } R^2 &= (t_1 + 3 - 2t_1 w_2)^2 + 8t_1(t_1 w_2 - 1). \end{aligned}$$

In the case of complete self mating, $t_1 = 0$, with $w_1 < 0.5$:

$$\begin{aligned} f &= (1 - 2w_1)/[2(2 - 3w_1)] \\ h_2 &= (1 - 2w_1)/(2 - 3w_1) \\ h_1 &= 1/[2(2 - 3w_1)], \end{aligned}$$

and only the trivial solution $h_1 = 1, h_2 = f = 0$ holds if $w_1 \geq 0.5$.

As in the previous model we calculate fitnesses of the three genotypes and find $w_1, 1, w_f = t_1 w_2 D_p/(D_o + D_p)$ for *Ms Ms, Ms ms* and *ms ms* respectively, when all genotypes are present. If male-steriles are absent we again

set $w_f = 0$. Of the total genetic contribution to the next generation by hermaphrodites the proportion $w_{hf} = D_p/(D_o + D_p)$ is still contributed through the ovules. When $w_1 = 1$, $t_1 \neq 0$ we again find that all three genotypes have equilibrium fitnesses of 1 for the non-trivial case $w_2 > 2/t_1$, and now $\hat{w}_{hf} = 1/t_1 w_2$. For $t_1 = 0$ and $w_1 < 0.5$, we have (equilibrium

TABLE 1

Frequencies of male-steriles, together with values for some other parameters, for equilibrium populations in the full-fitness model

w_1	w_2		s_1						
			0	0.1	0.3	0.5	0.7	0.95	1
0.8	1	f	0.077	0.075	0.071	0.063	0.050	0.021	0.012
		\hat{w}_f	0.478	0.478	0.479	0.481	0.485	0.494	0.496
		\hat{w}_{hf}	0.478	0.478	0.479	0.481	0.485	0.494	0.496
		\bar{W}	0.856	0.852	0.843	0.833	0.822	0.807	0.804
		s_2	0	0.092	0.276	0.464	0.659	0.926	0.985
0.8	1.2	f	0.098	0.097	0.095	0.091	0.085	0.072	0.068
		\hat{w}_f	0.559	0.560	0.560	0.561	0.564	0.569	0.570
		\hat{w}_{hf}	0.466	0.466	0.467	0.468	0.470	0.474	0.475
		\bar{W}	0.864	0.860	0.853	0.845	0.837	0.826	0.823
		s_2	0	0.087	0.263	0.439	0.620	0.856	0.906
0.5	1	f	0.214	0.216	0.220	0.223	0.227	0.232	0.233
		\hat{w}_f	0.429	0.428	0.426	0.424	0.422	0.420	0.419
		\hat{w}_{hf}	0.429	0.428	0.426	0.424	0.422	0.420	0.419
		\bar{W}	0.740	0.736	0.729	0.722	0.714	0.703	0.701
		s_2	0	0.075	0.223	0.369	0.512	0.687	0.721
0.5	1.2	f	0.237	0.239	0.243	0.247	0.251	0.255	0.256
		\hat{w}_f	0.491	0.490	0.487	0.485	0.482	0.479	0.478
		\hat{w}_{hf}	0.409	0.408	0.406	0.404	0.402	0.399	0.398
		\bar{W}	0.756	0.753	0.748	0.742	0.735	0.727	0.725
		s_2	0	0.069	0.205	0.339	0.470	0.630	0.662
1	3	f	0.250	0.250	0.250	0.250	0.250	0.250	0.250
		\hat{w}_f	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		\hat{w}_{hf}	0.333	0.333	0.333	0.333	0.333	0.333	0.333
		\bar{W}	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		s_2	0	0.050	0.150	0.250	0.350	0.475	0.500
1	20	f	0.474	0.474	0.474	0.474	0.474	0.474	0.474
		\hat{w}_f	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		\hat{w}_{hf}	0.050	0.050	0.050	0.050	0.050	0.050	0.050
		\bar{W}	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		s_2	0	0.005	0.016	0.026	0.037	0.050	0.053

fitnesses) $\hat{w}_f = 0$ and $\hat{w}_{hf} = 0.5$. The rates at which pollen grains from hermaphrodites take part in selfing and crossing are now $s_2 = s_1 D_p / D_o$ and $t_2 = 1 - s_2 = t_1 (D_p + w_2 f) / D_o$ respectively, but we stress that s_1 , t_1 and D_o have different values in the two models. We now have $s_2 < s_1$ as long as both t_1 and f are greater than zero.

(iii) Numerical results

A range of numerical values for proportions of male-steriles, and values of various fitness and outcrossing parameters, for equilibrium populations

under both models is given in tables 1 and 2. Values used for degree of selfing and for seed output of male-steriles relative to male-fertiles (w_2) were similar when possible to values found in the literature (table 3). Values for w_2 given in table 3 represent two situations, namely gynodioecy ($w_2 = 2$) and subdioecy ($w_2 = 9.8, 18.67$ and 21.4), since the latter high

TABLE 2

Frequencies of male-steriles, together with values for some other parameters, for equilibrium populations in the limited-fitness model

w_1	w_2		s_1						
			0	0.1	0.3	0.5	0.7	0.95	1
0.8	1	f	0.077	0.066	0.044	0.012	0	0	0
		\hat{w}_f	0.478	0.434	0.344	0.249	0	0	0
		\hat{w}_{hf}	0.478	0.482	0.491	0.498	0.500	0.500	0.500
		\hat{W}	0.856	0.848	0.830	0.807	0.800	0.800	0.800
		s_2	0	0.093	0.289	0.496	0.700	0.950	1.000
0.8	1.2	f	0.098	0.084	0.055	0.020	0	0	0
		\hat{w}_f	0.559	0.512	0.408	0.298	0	0	0
		\hat{w}_{hf}	0.466	0.474	0.486	0.496	0.500	0.500	0.500
		\hat{W}	0.864	0.855	0.836	0.812	0.800	0.800	0.800
		s_2	0	0.090	0.284	0.493	0.700	0.950	1.000
0.5	1	f	0.214	0.204	0.183	0.162	0.135	0.059	0
		\hat{w}_f	0.429	0.394	0.318	0.235	0.145	0.025	0
		\hat{w}_{hf}	0.429	0.438	0.455	0.470	0.484	0.499	0.500
		\hat{W}	0.740	0.727	0.700	0.668	0.626	0.537	0.500
		s_2	0	0.078	0.250	0.443	0.656	0.945	1.000
0.5	1.2	f	0.237	0.225	0.200	0.174	0.144	0.063	0
		\hat{w}_f	0.491	0.454	0.371	0.277	0.173	0.030	0
		\hat{w}_{hf}	0.409	0.420	0.442	0.462	0.480	0.498	0.500
		\hat{W}	0.756	0.743	0.714	0.679	0.634	0.540	0.500
		s_2	0	0.072	0.238	0.429	0.645	0.943	1.000
1	3	f	0.250	0.206	0.045	0	0	0	0
		\hat{w}_f	1.000	1.000	1.000	0	0	0	0
		\hat{w}_{hf}	0.333	0.370	0.476	0.500	0.500	0.500	0.500
		\hat{W}	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		s_2	0	0.059	0.273	0.500	0.700	0.950	1.000
1	20	f	0.474	0.471	0.462	0.444	0.400	0	0
		\hat{w}_f	1.000	1.000	1.000	1.000	1.000	0	0
		\hat{w}_{hf}	0.050	0.056	0.071	0.100	0.167	0.500	0.500
		\hat{W}	1.000	1.000	1.000	1.000	1.000	1.000	1.000
		s_2	0	0.006	0.023	0.056	0.140	0.950	1.000

values for relative seed output of the male-steriles imply near female sterility of "hermaphrodites" and their virtual conversion into males (Ross, 1970*b*).

Table 1 shows that under the full-fitness model, where male-steriles are maintained by slight overdominance with or without slight differential ovule fertility ($w_1, w_2 = 0.8, 1$, or $0.8, 1.2$), equilibrium proportions of male-steriles decline steadily with increased selfing among hermaphrodites, but with more pronounced overdominance ($w_1, w_2 = 0.5, 1$, or $0.5, 1.2$) there are increased equilibrium proportions of male-steriles with increased s_1 . Where male-steriles are favoured by increased seed output only ($w_1 = 1$,

$w_2 > 1$) equilibrium proportions are not affected by degree of selfing among hermaphrodites. In contrast, under the limited-fitness model (table 2) increased s_1 is always accompanied by decreased equilibrium proportions of male-steriles. These are present at equilibrium when there is a relatively slight degree of selfing among hermaphrodites ($s_1 = 0.1, 0.3$), but are lost as degree of selfing becomes moderate or intense ($s_1 \geq 0.5$). When $s_1 = 1$, they are present at equilibrium only if $w_1 < 0.5$. Comparison of the two models indicates the importance of the efficiency of the cross-pollination mechanism for the survival of the male-steriles. Both models show that slight inbreeding among hermaphrodites ($s_1 = 0.1$) may have little or no

TABLE 3
Some actual values of s_1 , w_1 and w_2 similar to those used in this paper

Species	Author	s_1	w_1	w_2	Notes
<i>Plantago lanceolata</i>	Ross (1970a)	0	—	—	Gynodioecious and self-incompatible
<i>Collinsia heterophylla</i>	Weil and Allard (1964)	0.06, 0.13*	—	—	Self-compatible
<i>Clarkia exilis</i>	Vasek (1964)	0.555	—	—	Flower structure apparently adapted to inbreeding
<i>Vicia faba</i>	Fyfe and Bailey (1951)	0.688	—	—	
Barley	Jain and Allard (1960)	0.98 to 0.99	—	—	
<i>Pimelea traversii</i>	Burrows (1960, 1962)	—	1	2†	Gynodioecious
<i>P. prostrata</i>	Burrows (1960, 1962)	—	1	9.8†	Near dioecious
<i>Cortaderia selloana</i>	Connor (1973)	—	1	18.67‡	Near dioecious
<i>Pimelea sericeo-villosa</i>	Burrows (1960, 1962)	—	1	21.4†	Near dioecious

* Weil and Allard (1964) gave 6 estimates for degree of outcrossing. The two chosen here are 0.94 ± 0.27 and 0.87 ± 0.51 .

† Fruit production.

‡ Includes differential seed germination.

effect on equilibrium proportions of male-steriles. Even when s_1 reaches 0.5 effects of selfing among hermaphrodites are not very marked under the full-fitness model.

We now consider the behaviour of some other parameters represented in tables 1 and 2. Under the full-fitness model with overdominance fitness of the male-steriles at equilibrium, \hat{w}_j , declines when there are increased equilibrium proportions of male-steriles, \hat{f}_j , with increased s_1 , and increases when there is decreased \hat{f}_j with increased s_1 . Male-steriles are often less than half as fit as hermaphrodites at equilibrium. Under the limited-fitness model with overdominance, increased s_1 is accompanied by decreased \hat{w}_j with decreased \hat{f}_j . Under both models, where male-steriles are maintained only by differential ovule fertility ($w_1 = 1$, $w_2 = 3, 20$), $\hat{w}_j = 1$ at equilibrium, as demonstrated above. In equilibrium populations, when there

is overdominance, the proportion of the total offspring of hermaphrodites left through the ovules, \hat{w}_{hf} is usually not much less than 0.5 for both models (e.g. full-fitness model, $w_1 = 0.8$, $w_2 = 1$, $s_1 = 0.5$, $\hat{w}_{hf} = 0.481$; $w_1 = 0.5$, $w_2 = 1$, $s_1 = 0.1$, $\hat{w}_{hf} = 0.428$), indicating that in a gynodioecious system the hermaphrodites may still largely function both as female and as male (cf. Lloyd, 1974*b*). For both models, the mean population fitness at equilibrium, \bar{W} , is given by $\hat{w}_1\hat{h}_1 + \hat{h}_2 + \hat{w}_2\hat{f}$, and always equals 1 when male-steriles are maintained only by increased ovule fertility. When there is overdominance \bar{W} decreases steadily with increased selfing among hermaphrodites until male-steriles are eliminated.

3. DISCUSSION

Both models differ from that of Ho and Ross (1973) by assuming that the disadvantage of homozygotes at the M_s locus does not affect the ovule fertility of the male-steriles. Of the present models, the full-fitness model may be more appropriate to moderately or largely outbreeding populations (probably many gynodioecious populations) with which this paper is primarily concerned, since the assumption of full seed set on the male-steriles implies the presence of an efficient cross-pollination mechanism. The limited-fitness model is useful for comparison and may better represent extreme inbreeders. For inbreeding populations Jain (1961) presented a model where outcrossing rates of male-steriles were greater than those of hermaphrodites, but where some values used for these rates implied insufficient pollination of male-steriles, as occurs for example in male-sterile barley mutants (Suneson, 1951).

Our results may have some relevance to the evolution of gynodioecy. It does not seem likely that newly arisen male-sterile mutants would have the more than doubled seed fertility with respect to hermaphrodites required for the mutants to persist at levels greater than those attributable to a balance between recurrent mutation and selection. In contrast, these results and those of Ho and Ross (1973) show that even conservative values for overdominance at the male-sterility locus may be associated with appreciable equilibrium proportions of male-steriles. Once the male-steriles were firmly established in the population further evolution of the system could occur, perhaps by accumulation of genes which increased relative seed fertility of male-steriles.

The present results suggest that new male-sterile mutants may sometimes be more easily established in populations that are already outbred, and the results may therefore have some relevance to the situation in *Plantago* (Baker, 1963; Ross, 1970*a*) and other genera (Young, 1972; Horovitz and Galil, 1972), where some species are both self-incompatible and gynodioecious, and where the presence of the male-steriles is presumably not associated with any increase in crossing.

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