

# Fixation of Advantageous Alleles in Partially Self-Fertilizing Populations: The Effect of Different Selection Modes

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## ABSTRACT

The expected fixation probability of an advantageous allele was examined in a partially self-fertilizing hermaphroditic plant species using the diffusion approximation. The selective advantage of the advantageous allele was assumed to be increased viability, increased fecundity, or an increase in male fitness. The mode of selection, as well as the selfing rate, the population size, and the dominance of the advantageous allele, affect the fixation probability of the allele. In general it was found that increases in selfing rate decrease the fixation probability under male sexual selection, increase fixation probability under fecundity selection, and increase when recessive and decrease when dominant under viability selection. In some cases the highest fixation probability of advantageous alleles under fecundity or under male sexual selection occurred at an intermediary selfing rate. The expected mean fixation times of the advantageous allele were also examined using the diffusion approximation.

**M**ANY plants are partially self-fertilizing (Schemske and Lande 1985; Cruden and Lyon 1989), and the evolutionary processes depend critically on the selfing rate (Bennett and Binet 1956; Allard *et al.* 1968; Ohta and Cockerham 1974; Gregorius 1982; Caballero and Hill 1992b; Caballero *et al.* 1992; Charlesworth 1992; Pollak and Sabran 1992; Damgaard *et al.* 1994). The fate of a new advantageous mutation can to some degree be predicted from knowledge of the fixation probability and the expected fixation time of the mutation. Lately, estimation of fixation probability and the expected fixation time of advantageous alleles has also become important in the risk evaluation of genetically modified plants, *i.e.*, to estimate the probability that a transgene will be introgressed into a wild plant population (Damgaard 1999; Kjær *et al.* 1999).

In this study I focus on hermaphroditic plants, *i.e.*, plants with both male and female reproductive organs. Often the two sexes are structurally close together, but the different structures have distinctly different functions and consequently are under different selective pressures (Lloyd and Bawa 1984). For example, there is a general tendency that selfing plant populations, due to selective forces, have less pollen than outcrossing hermaphroditic plant populations (*e.g.*, Charlesworth and Charlesworth 1981; Cruden and Lyon 1985).

An advantageous allele may affect the different fitness components in different ways. An advantageous "general household" mutation may have a positive effect on plant viability and fecundity (seed production) but has

no effect on male sexual selection (*e.g.*, attractiveness to pollinating insects and number of pollen). Conversely, a color mutation that makes the flower more attractive to pollinating insects may have a positive effect on male sexual selection but no effect on viability. Perhaps there may even be a trade-off, so that a mutation that increases attractiveness to pollinating insects and thereby increases male sexual selection also increases the probability that herbivorous insects visit the plant so that viability is reduced.

The fitness components in hermaphroditic plants have been shown to be only loosely correlated. For example, although it is difficult to measure paternal fitness, it seems that fecundity and paternal fitness are not strongly correlated and in some cases are negatively correlated (Ross 1990). Plant viability and fecundity depend strongly on abiotic and biotic factors, whereas the variation in paternal function, at least in some cases, is observed to be lower than the variation in female functioning (Stephenson and Bertin 1983; Mazer 1987; Schlichting and Devlin 1989).

An advantageous allele that either by a mutation, migration, or hybridization event is introduced into a plant population may become fixed in the population. The fixation probability of the advantageous allele depends on the selective advantage of the allele, the coefficient of dominance, the effective population size, and the demography of the population (Haldane 1927; Caballero and Hill 1992b; Otto and Whitlock 1997). The effects of partial self-fertilization on fixation probabilities and fixation times of advantageous alleles have been examined in the case of viability selection (Caballero and Hill 1992b; Charlesworth 1992; Pollak and Sabran 1992). However, the fixation process of advanta-

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geous alleles under other modes of selection may show a different relationship with selfing rate. Viability selection on hermaphroditic plants affects both sexes equally (symmetric selection), whereas fecundity selection and male sexual selection affect the two sexes differently (asymmetric selection). The difference between symmetric and asymmetric selection and the evolutionary consequences have received little attention (although see Bodmer 1965; Feldman *et al.* 1983), and the interaction between selection mode and mating system on the fixation process of advantageous alleles has to my knowledge not been investigated before.

Here, the effect of viability selection is compared with fecundity selection and male sexual selection on the fixation probability and the expected fixation time of an advantageous allele in a partially self-fertilizing plant population.

#### MODEL

Consider a single locus in a finite partially self-fertilizing hermaphroditic plant population of census size  $N$ . The population is a mixed mating Fisher-Wright population, where the number of offspring is Poisson distributed, and a fraction  $s$  of new zygotes are produced by self-fertilization and a fraction  $1 - s$  by random mating. The population is assumed to be initially fixed for the allele  $A_2$ , except for a single copy of a new advantageous mutation  $A_1$ .

Each generation starts by the production of zygotes from gametes. Before selection, the frequency of the  $A_1$  allele among male and female gametes is  $p_m$  and  $p_f$ , respectively, and the frequency of the  $A_2$  allele among male and female gametes is  $q_m = 1 - p_m$  and  $q_f = 1 - p_f$ , respectively. Assuming weak selection, the population has an equilibrium coefficient of inbreeding  $F^* = s/(2 - s)$  (Haldane 1924), and because the equilibrium is reached relatively quickly (Wright 1969; Nordborg and Donnelly 1997), the proportions of the three genotypes  $A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  before selection, denoted by  $u$ ,  $v$ , and  $w$ , can be expressed as

$$\begin{aligned} u &= (1 - s)p_m p_f + s\left(u_f + \frac{v_f}{4}\right) \\ v &= (1 - s)(p_m q_f + q_m p_f) + s\left(\frac{v_f}{2}\right) \\ w &= (1 - s)q_m q_f + s\left(w_f + \frac{v_f}{4}\right), \end{aligned} \quad (1)$$

where  $u_f = p_f^2 + F^* p_f q_f$ ,  $v_f = 2p_f q_f - 2F^* p_f q_f$ , and  $w_f = q_f^2 + F^* p_f q_f$ . The frequency of the  $A_1$  allele in the population before selection takes place is

$$p = u + \frac{v}{2} = \frac{p_f + s p_f + (1 - s)p_m}{2}. \quad (2)$$

Only genotypic selection is assumed to operate in the system, and the relative fitness of the three genotypes

TABLE 1

The relative fitness of the three genotypes

Genotype	Viability selection	Fecundity selection	Male sexual selection
$A_1A_1$	$1 + sv$	$1 + sf$	$1 + sm$
$A_1A_2$	$1 + hvsv$	$1 + hfsf$	$1 + hmsm$
$A_2A_2$	1	1	1

$A_1A_1$ ,  $A_1A_2$ , and  $A_2A_2$  is shown in Table 1. Viability selection is assumed to take place before reproduction and affects both sexes of the hermaphroditic plant equally, fecundity selection operates on the number of seeds produced by the plants, and male sexual selection operates on the number of foreign pollination events taking place, disregarding the pollen needed for selfing events. Note that the term fecundity selection normally includes gametic selection during zygote formation (*e.g.*, Feldman *et al.* 1983), but because gametic selection is assumed not to take place, the selection forces can be adequately described by the frequency of the advantageous allele in the female and male gamete pool.

After selection, the frequency of  $A_1$  among the male gametes is

$$p'_m = \frac{u'_m + \frac{1}{2} v'_m}{u'_m + v'_m + w'_m}, \quad (3a)$$

where  $u'_m = u(1 + sv)(1 + sm)$ ,  $v'_m = v(1 + hvsv)(1 + hmsm)$ , and  $w'_m = w$ . Likewise, after selection, the frequency of  $A_1$  among the female gametes is

$$p'_f = \frac{u'_f + \frac{1}{2} v'_f}{u'_f + v'_f + w'_f}, \quad (3b)$$

where  $u'_f = u(1 + sv)(1 + sf)$ ,  $v'_f = v(1 + hvsv)(1 + hfsf)$ , and  $w'_f = w$ .

The frequency of the  $A_1$  allele among the newly formed zygotes in the next generation,  $p'$ , can be calculated by inserting  $p'_m$  and  $p'_f$  into Equation 2. To express the change in the frequency of the  $A_1$  allele,  $p' - p$ , by a single variable,  $p'_m$  is approximated by a function of  $p'_f$ . The frequency of the advantageous allele among the male gametes is expressed by the ratio between the frequencies in male and female gametes when the advantageous allele is rare:

$$p'_m \approx \left(\lim_{p'_m, p'_f \rightarrow 0} \frac{p'_m}{p'_f}\right) p'_f = \frac{1 + hmsm}{1 + hfsf} p'_f. \quad (4)$$

This approximation (4) is motivated by the fact that the fate of a positively selected allele is determined when the allele is rare (especially true for dominant alleles or highly selfing populations).

The expected fixation probability and the mean fixation time in a finite population of census size  $N$  can be calculated from the expected change in allele frequency,  $M = p' - p$ , and the mean variance of the

change,  $V = p(1 - p)/2N_e$ , using the diffusion approximation (Kimura 1962). The effective population size,  $N_e$ , in a partial selfing population, where the number of offspring is Poisson distributed, is  $N(2 - s)/2$  (Caballero and Hill 1992a). Because we assumed that initially only a single copy of the  $A_1$  allele is present, the fixation probability of the advantageous allele is calculated by

$$P = \frac{\int_0^{1/2N} G(x) dx}{\int_0^1 G(x) dx}, \quad (5)$$

where  $G(x) = \exp(-\int(2M/V)dx)$  (Kimura 1962). Correspondingly, the mean time to fixation is calculated by

$$T = \int_{1/2N}^1 \frac{4N_e P}{x(1-x)G(x)} \left( \int_x^1 G(t) dt \right) dx \quad (6)$$

(Ewens 1963, 1969).

An alternative heuristic approximation of the fixation probability of an advantageous allele under viability selection in a large partially selfing population has been given by Caballero and Hill (1992b). The fixation probability is approximately  $2sv(F^* + hv - F^*hv)$ , and similar approximations can be made for the fixation probability of alleles under fecundity and male sexual selection, *i.e.*,  $sf(F^* + hf - F^*hf)(1 + m)$  and  $sm(F^* + hm - F^*hm)(1 - m)$ , respectively, where  $m = 2F^*/(1 + F^*)$  is the correlation between the frequencies of alleles in the mates.

In the following I show only results from the diffusion approximation Equations 5 and 6, because this approximation is the most precise. Equations 5 and 6 were solved numerically using the *NIntegrate* procedure in Mathematica (Wolfram 1996), and the results were checked by stochastic simulations of a mixed-mating Fisher-Wright population with viability, fecundity, and male sexual selection. Simulations started with a single copy of the advantageous allele in one out of  $N$  diploid individuals and the selection forces were operating in the gamete pool as described by Equation 3. The stochastic simulation program was checked in the neutral case, where both fixation probabilities and mean fixation times behaved as expected according to neutral theory. The stochastic simulations of the fixation probabilities and mean fixation times are reported as the means of 10,000 simulations and 95% confidence intervals. The confidence intervals were in the case of the fixation probability constructed under the assumption that fixation of the advantageous allele was a binomial-distributed process, and in the case of fixation times as the interval between the 26th and 975th of 1000 ordered bootstrap samples.

## RESULTS

The expected change in the frequency of the advantageous allele depends on the selection mode, the domi-

nance of the advantageous allele, and the selfing rate (Figure 1). As seen from Equation 3, viability selection operates in both sexes, whereas fecundity and male sexual selection operate only in the female and male sexes, respectively; therefore, viability selection is generally more effective than the other two selection modes. When the selfing rate is zero, viability selection is twice as effective as both fecundity and male sexual selection, which have equal effect (Figure 1; due to the approximation in Equation 4, this is exactly the case only for  $h = 0$ ). However, from Equation 2 it is apparent that, as the selfing rate increases, the importance of the female function increases, and when the selfing rate is one, viability and fecundity selection have the same effect. Conversely, when the selfing rate is increased, the importance of the male function decreases, and when the selfing rate is one, the male sexual selection is without any effect, *i.e.*, the expected change in allele frequency is zero, and the advantageous allele is effectively neutral (Figure 1). To illustrate this, imagine a mutation that increases the amount of pollen by 10% in a wind-pollinated plant species ( $sm = 0.1$ ) so that a relatively large proportion of the pollen in the male gamete pool has this mutation. Such a mutation may be selectively favored in an outcrossing population, whereas it will be disfavored in a selfing population, because the size of the male gamete pool is without evolutionary importance (providing that there are sufficient pollen grains to effect self-fertilization).

When the advantageous allele is recessive, the fixation probability depends critically on the selfing rate because the selective advantage is expressed only in  $A_1A_1$  homozygotes. Increasing selfing increases the proportion of homozygotes, and the expected change in allele frequency is an increasing function of selfing rate when the advantageous allele is under viability and fecundity selection (Figure 1,  $h = 0$ ), and the fixation probabilities are increasing functions of selfing rate (Figure 2,  $h = 0$ ; Caballero and Hill 1992b; Charlesworth 1992). A recessive advantageous allele under male sexual selection has two opposing forces acting on it. Increased selfing increases the proportion of homozygotes but also reduces the importance of the male function, and the fixation probability of the allele is a concave function of selfing rate, so that, for  $sm = 0.1$  and  $N \geq 100$ , a recessive advantageous allele has a maximal fixation probability at an intermediary selfing rate.

The fate of a positively selected dominant allele is determined when the allele is rare (Haldane 1927; Otto and Whitlock 1997), and it is interesting that the role of selfing on the expected change in allele frequency for a dominant advantageous rare allele is qualitatively different for the three selection modes. For viability selection, the expected change in allele frequency for low frequencies is almost independent of selfing rate. Whereas, the expected change in allele frequency for low frequencies increases with selfing rate

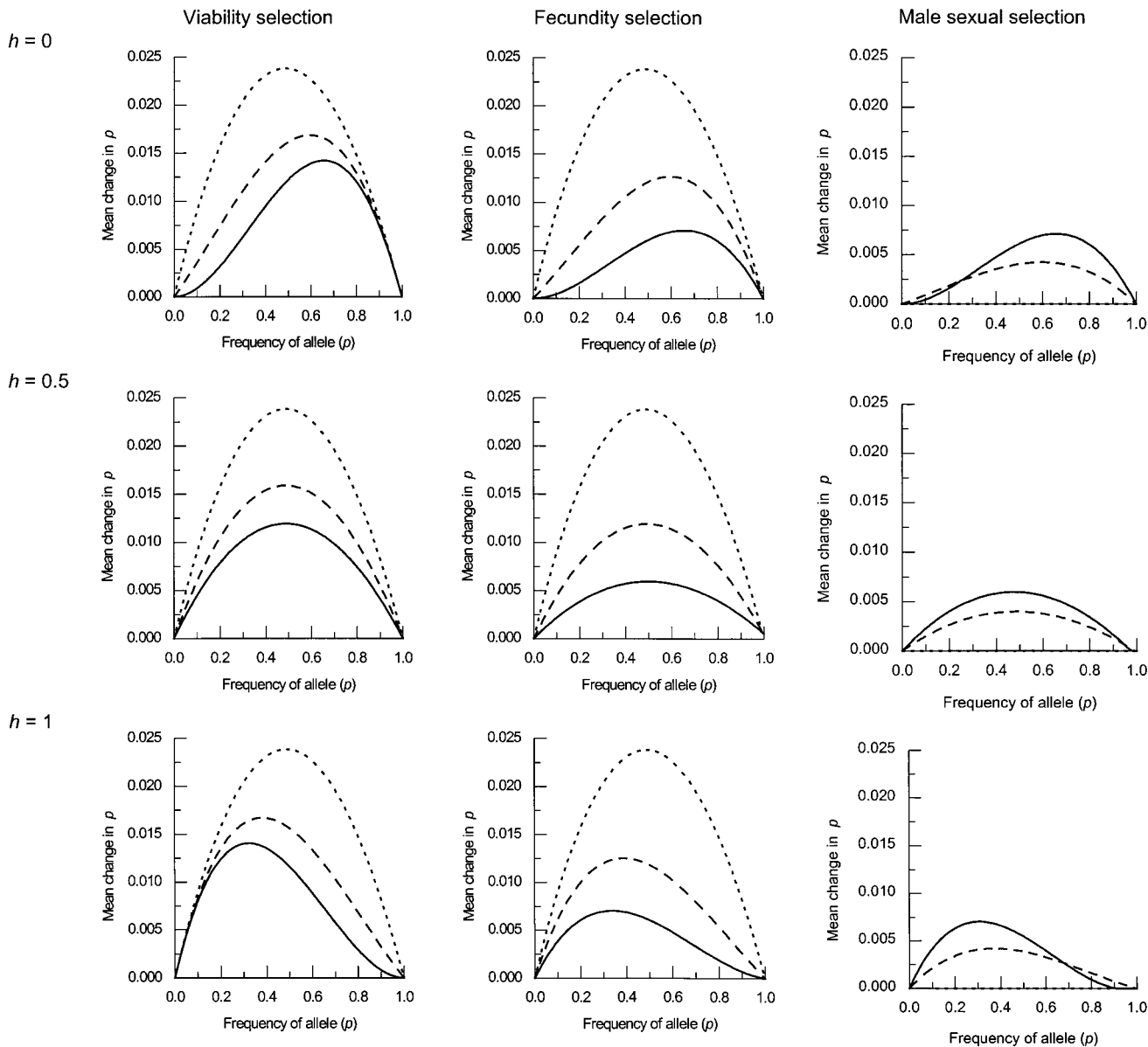


Figure 1.—The expected mean change in the frequency of the advantageous allele as a function of the allele frequency ( $p$ ) for different selfing rates ( $s$ ) and dominance levels ( $h$ ). (—)  $s = 0$ ; (---)  $s = 0.5$ ; (···)  $s = 1$ . Viability selection,  $sv = 0.1$ ,  $sf = 0$ ,  $sm = 0$ ; fecundity selection,  $sv = 0$ ,  $sf = 0.1$ ,  $sm = 0$ ; male sexual selection,  $sv = 0$ ,  $sf = 0$ ,  $sm = 0.1$ .

for fecundity selection and decreases for male sexual selection (Figure 1,  $h = 1$ ). This qualitative difference in expected change in allele frequency when the allele is rare, and the increased importance of the female function with increasing selfing rate, explain the difference in the fixation probabilities among the different selection modes. The fixation probability of the advantageous allele under viability selection decreases approximately linearly with selfing rate (Caballero and Hill 1992b; Charlesworth 1992), whereas the fixation probability of the allele under fecundity selection is a concave function of selfing rate and a convex function of selfing rate when the allele is under male sexual selection (Figure 2,  $h = 1$ ). The decrease in fixation

probability with selfing under viability selection, even though the expected change in allele frequency when the allele is rare is almost independent of selfing rate, is caused by a lower proportion of heterozygotes and increased genetic drift. Note also that, for  $sf = 0.1$  and  $N \geq 100$ , the advantageous allele has a maximal fixation probability at an intermediary selfing rate.

The case of codominance,  $h = 0.5$ , is interesting, because it is a transition point of the functional behavior of the expected change in allele frequency as a function of allele frequency and the fixation probability as a function of selfing rate. When the advantageous allele is codominant, the expected change in allele frequency is highest at the allele frequency 0.5. Whereas, if the

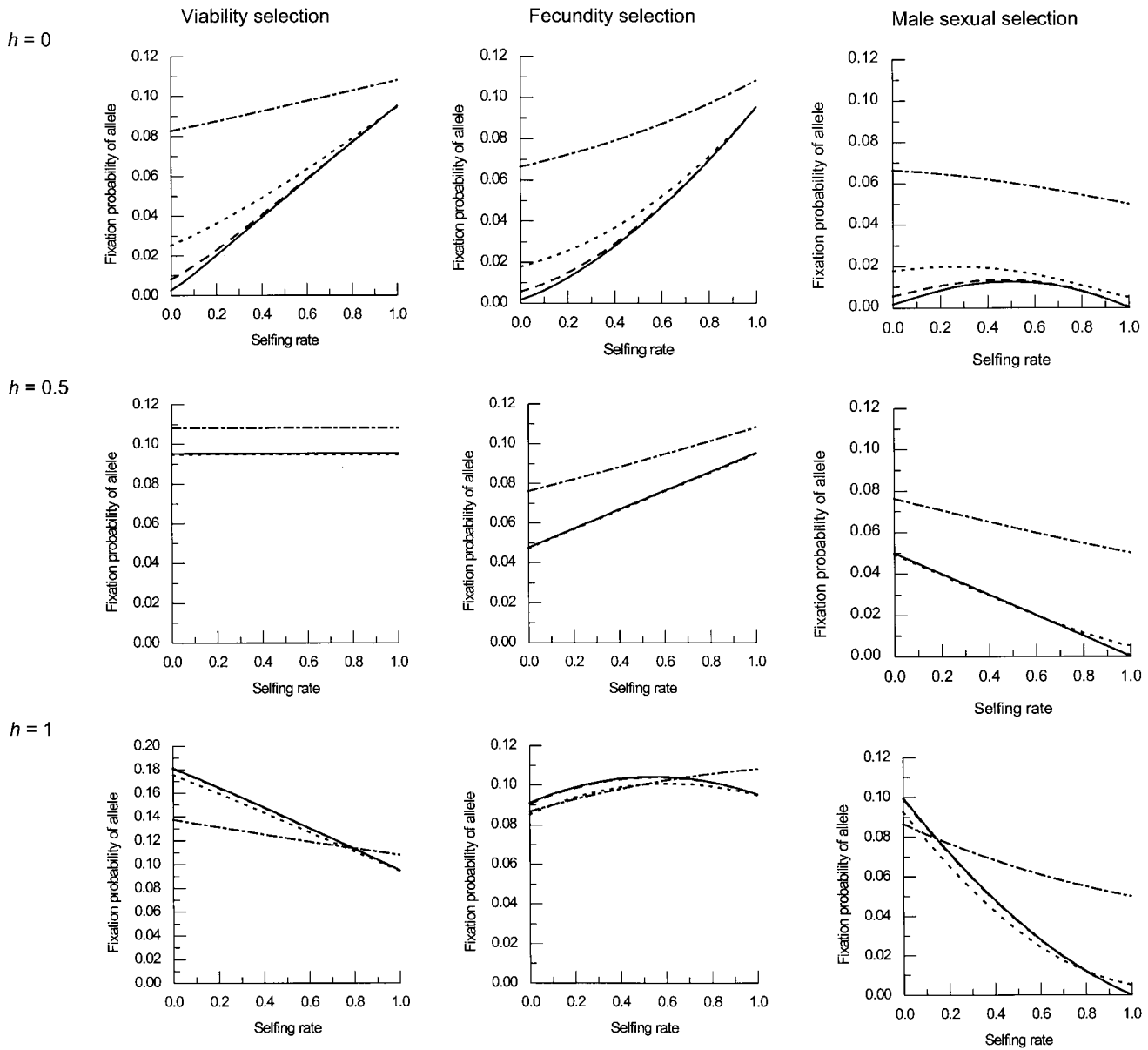


Figure 2.—The expected fixation probability of the resistance allele as a function of selfing rate ( $s$ ) for different values of the census population size ( $N$ ). (· · ·)  $N = 10$ ; (---)  $N = 100$ ; (- · - ·)  $N = 1000$ ; (—)  $N = 10,000$ . Viability selection,  $sv = 0.1$ ,  $sf = 0$ ,  $sm = 0$ ; fecundity selection,  $sv = 0$ ,  $sf = 0.1$ ,  $sm = 0$ ; male sexual selection,  $sv = 0$ ,  $sf = 0$ ,  $sm = 0.1$ .

allele is recessive and the selfing rate is less than one, the expected change in allele frequency is highest at a frequency  $>0.5$ , and if the allele is dominant and the selfing rate is less than one, the expected change in allele frequency is highest at a frequency  $<0.5$  (Figure 1). Correspondingly, when the advantageous allele is codominant, the fixation probability for an advantageous allele under viability selection is the turning point where the fixation probability goes from being an increasing function of selfing rate when the allele is recessive to a decreasing function when the allele is dominant (Caballero and Hill 1992b; Charlesworth 1992). For an advantageous allele under fecundity selection,

codominance is the point where the fixation probability goes from being a convex function of selfing rate when the allele is recessive to a concave function when the allele is dominant. Conversely, for an advantageous allele under male sexual selection, codominance is the point where the fixation probability goes from being a concave function to a convex function (Figure 2).

The fixation probability was also calculated for other parameter values than shown in results. Generally, it can be concluded that the functional relationship of the fixation probability with selfing rate, except for a constant factor, depends only on the combined parameter  $Nsx$ , where  $sx$  is the selection coefficient. If the fixa-

tion probability is expressed relative to the neutral fixation rate ( $1/2N$ ), the relative fixation probability is approximately equal for different cases with equal  $Nsx$ .

If the different selection modes are combined, the functional dependency of the fixation probability on selfing rate is a mixture of the three selection modes. Generally, viability selection is more important than the other modes of selection, because it is assumed to operate on both male and female gametes, and the influence of male sexual selection decreases with selfing rate.

The probability of fixation depends on the census number of plants in the population as well as on the mating system (Figure 2). Small populations of plants have generally higher fixation probabilities of advantageous alleles compared to larger population sizes (Caballero and Hill 1992b; Charlesworth 1992). However, when the advantageous allele is dominant, the fixation probability may increase with population size (Caballero and Hill 1992b; Charlesworth 1992). This effect is not caused by inadequacy of the diffusion approximation, because the effect also was observed in the stochastic simulations (*e.g.*, viability selection,  $s = 0$ ,  $h = 1$ ; 95% confidence intervals;  $N = 10$ , 0.125–0.138;  $N = 100$ , 1000, or 10,000, 0.161–0.186). When  $Ns$  is of the order of 100, the fixation probability was close to an asymptotic value of the fixation probability, and the probability of fixation did not change much with a further increase in population size.

In general, it can be concluded that increases in selfing rate decrease the fixation probability under male sexual selection, increase fixation probability under fecundity selection, and increase when recessive and decrease when dominant under viability selection.

The expected fixation times of advantageous alleles under the different selection modes were calculated using the diffusion approximation in Equation 6 (Table 2). For an advantageous allele under viability selection, the expected fixation time in a random mating population increases with the coefficient of dominance, because the larger the effect of the heterozygotes, the longer it takes to lose the unfavorable allele (Caballero and Hill 1992b). The effect of increasing the selfing rate is to reduce the proportion of heterozygotes, and consequently, to reduce fixation times and to reduce the effect of dominance on the fixation time, until, in a purely selfing population, the expected fixation time is independent of the coefficient of dominance (Caballero and Hill 1992b). For an advantageous allele under fecundity selection, the effect of dominance and selfing rate on the expected fixation time is similar to an advantageous allele under viability selection, except that the expected fixation time generally is higher because the selection forces are smaller. In a purely selfing population, where the selection forces are equal for an allele under viability and fecundity selection, the fixation times are also equal. For an advantageous allele under male sexual selection, the situation is more complicated

because the importance of male sexual selection decreases with selfing rate until it is effectively neutral in a purely selfing population. In random mating populations, the fixation time is still an increasing function of the coefficient of dominance, but the expected fixation time is not a strictly decreasing function of selfing rate in populations with intermediary and large  $Ns$ . Instead, the expected fixation time for some parameter values is a convex function of selfing rate and the smallest expected fixation time occurs at an intermediary selfing rate.

The results of the diffusion approximations were checked by stochastic simulations (Table 2). Generally, the diffusion approximations are satisfactory, and the stochastic simulations confirmed the qualitative differences among the fixation probabilities and the expected fixation times for the three selection modes observed using the diffusion approximations. However, there were some cases (denoted by a solid box in Table 2) where the diffusion approximations for most  $N$  were outside the 95% confidence interval, and it can be concluded that the diffusion approximation is imprecise for recessive advantageous alleles under viability and fecundity selection in highly selfing populations and for dominant advantageous alleles under fecundity and male sexual selection in outcrossing populations.

## DISCUSSION

The mode of selection has previously been shown to have an effect on the evolution of a trait (Bodmer 1965; Feldman *et al.* 1983). In this study, three different modes of selection—viability, fecundity, and male sexual selection—have been compared for an advantageous allele in a mixed mating population. Viability selection on hermaphroditic plants affects both sexes, whereas fecundity and male sexual selection affect only one of the sexes, and because the male gamete in a selfing event shares the parent of the female gamete, it is not surprising that the fixation probability for different selfing rates differs among the different modes of selection. It is assumed that viability selection affects both sexes equally; however, in some plant species gender allocation is a function of plant size (Lloyd and Bawa 1984), and because small plants are expected to have a relatively high mortality, the assumption of equal effect of viability selection on both sexes can be criticized.

In this study, only selection forces operating on genotypes (genotypic selection) are considered, and the effect of gametic selection on female and male gametes has not been included. This is motivated by the fact that one of the main effects of selfing is to alter the genotypic proportions toward increased homozygosity. Another effect of selfing is to decrease the importance of the male gamete, so that, in a purely selfing population, alleles expressed only in the male gametes are effectively neutral (Damgaard *et al.* 1994).

Plant species in a changing environment that fix ad-

TABLE 2

Viability selection, fecundity selection, and male sexual selection: comparison between the diffusion approximations and stochastic simulations

		Selfing rate: 0				Selfing rate: 0.5				Selfing rate: 1			
		<i>P</i> (fixation)		Fixation time		<i>P</i> (fixation)		Fixation time		<i>P</i> (fixation)		Fixation time	
		Diff. <sup>a</sup>	Sim. <sup>b</sup>	Diff. <sup>c</sup>	Sim. <sup>d</sup>	Diff.	Sim.	Diff.	Sim.	Diff.	Sim.	Diff.	Sim.
Viability selection <sup>e</sup>													
<i>h</i> = 0	<i>N</i> = 10	0.083	0.080	0.82	0.81	0.095	0.089	0.65	0.64	0.108	0.098	0.45	0.45
	<i>N</i> = 100	0.025	0.025	0.35	0.35	0.056	0.050	0.26	0.26	0.095	0.084	0.18	0.18
	<i>N</i> = 1,000	0.0080	0.0073	0.095	0.010	0.050	0.040	0.050	0.049	0.095	0.082	0.030	0.030
	<i>N</i> = 10,000	0.0025	0.0029	0.026	0.026	0.049	0.044	0.0073	0.0072	0.095	0.079	0.0042	0.0042
<i>h</i> = 0.5	<i>N</i> = 10	0.108	0.101	0.91	0.92	0.108	0.102	0.68	0.67	0.108	0.104	0.45	0.45
	<i>N</i> = 100	0.095	0.093	0.36	0.36	0.095	0.096	0.27	0.27	0.095	0.087	0.18	0.18
	<i>N</i> = 1,000	0.095	0.096	0.061	0.061	0.095	0.091	0.045	0.045	0.095	0.086	0.030	0.030
	<i>N</i> = 10,000	0.095	0.093	0.0085	0.0084	0.095	0.086	0.0064	0.0064	0.095	0.087	0.0042	0.0042
<i>h</i> = 1	<i>N</i> = 10	0.137	0.132	1.01	0.99	0.122	0.123	0.72	0.71	0.108	0.109	0.45	0.45
	<i>N</i> = 100	0.175	0.175	0.47	0.48	0.135	0.126	0.29	0.30	0.095	0.097	0.18	0.18
	<i>N</i> = 1,000	0.181	0.169	0.13	0.13	0.139	0.136	0.051	0.052	0.095	0.099	0.030	0.030
	<i>N</i> = 10,000	0.181	0.179	0.036	0.036	0.139	0.132	0.0076	0.0077	0.095	0.094	0.0042	0.0042
Fecundity selection <sup>f</sup>													
<i>h</i> = 0	<i>N</i> = 10	0.066	0.063	0.89	0.88	0.083	0.078	0.67	0.65	0.108	0.095	0.45	0.45
	<i>N</i> = 100	0.018	0.020	0.51	0.51	0.044	0.047	0.32	0.31	0.095	0.080	0.18	0.18
	<i>N</i> = 1,000	0.0056	0.0047	0.14	0.14	0.038	0.035	0.063	0.062	0.095	0.080	0.030	0.030
	<i>N</i> = 10,000	0.0018	0.0016	0.038	0.039	0.037	0.034	0.0094	0.0094	0.095	0.078	0.0042	0.0043
<i>h</i> = 0.5	<i>N</i> = 10	0.076	0.076	0.93	0.89	0.091	0.089	0.69	0.69	0.108	0.100	0.45	0.44
	<i>N</i> = 100	0.047	0.048	0.54	0.57	0.071	0.068	0.32	0.33	0.095	0.094	0.18	0.18
	<i>N</i> = 1,000	0.048	0.045	0.092	0.11	0.072	0.069	0.052	0.058	0.095	0.091	0.030	0.030
	<i>N</i> = 10,000	0.048	0.049	0.012	0.015	0.072	0.068	0.0065	0.0082	0.095	0.090	0.0042	0.0042
<i>h</i> = 1	<i>N</i> = 10	0.087	0.084	0.98	0.97	0.100	0.104	0.72	0.72	0.108	0.114	0.45	0.44
	<i>N</i> = 100	0.085	0.087	0.65	0.67	0.100	0.108	0.35	0.35	0.095	0.102	0.18	0.18
	<i>N</i> = 1,000	0.091	0.092	0.15	0.19	0.104	0.106	0.063	0.067	0.095	0.095	0.030	0.030
	<i>N</i> = 10,000	0.091	0.091	0.027	0.053	0.104	0.103	0.0093	0.0099	0.095	0.098	0.0042	0.0042

(continued)

Fixation of Advantageous Alleles

**TABLE 2**  
(Continued)

		Selfing rate: 0				Selfing rate: 0.5				Selfing rate: 1			
		<i>P</i> (fixation)		Fixation time		<i>P</i> (fixation)		Fixation time		<i>P</i> (fixation)		Fixation time	
		Diff. <sup>a</sup>	Sim. <sup>b</sup>	Diff. <sup>c</sup>	Sim. <sup>d</sup>	Diff.	Sim.	Diff.	Sim.	Diff.	Sim.	Diff.	Sim.
Male sexual selection <sup>e</sup>													
<i>h</i> = 0	<i>N</i> = 10	0.066	0.064	0.89	0.90	0.060	0.059	0.70	0.71	0.05	0.050	<u>0.48</u>	0.45
	<i>N</i> = 100	0.018	0.018	0.51	0.51	0.018	0.016	0.55	0.56	0.005	0.0056	0.50	0.55
	<i>N</i> = 1,000	0.0056	0.0044	0.14	0.13	<u>0.013</u>	0.011	0.14	0.14	0.0005	0.0006	0.50	0.49
	<i>N</i> = 10,000	0.0018	0.0025	0.038	0.041	0.013	0.012	0.024	0.02	0.00005	—	0.50	—
<i>h</i> = 0.5	<i>N</i> = 10	0.076	0.076	<u>0.95</u>	0.93	0.062	0.061	<u>0.71</u>	0.74	0.05	0.052	0.48	0.49
	<i>N</i> = 100	0.049	0.049	<u>0.61</u>	0.58	0.025	0.025	<u>0.60</u>	0.59	0.005	0.0038	0.50	0.47
	<i>N</i> = 1,000	0.050	0.048	NC	0.11	0.025	0.026	<u>0.16</u>	0.14	0.0005	0.0004	0.50	0.44
	<i>N</i> = 10,000	0.050	0.047	NC	0.015	0.025	0.024	NC	0.021	0.00005	—	0.50	—
<i>h</i> = 1	<i>N</i> = 10	0.087	0.090	<u>1.00</u>	0.95	0.064	0.063	0.72	0.72	0.05	0.048	0.48	0.46
	<i>N</i> = 100	0.093	0.087	<u>0.76</u>	0.69	<u>0.033</u>	0.037	0.65	0.66	0.005	0.0038	0.50	0.44
	<i>N</i> = 1,000	<u>0.099</u>	0.093	<u>0.32</u>	0.19	<u>0.037</u>	0.036	<u>0.16</u>	0.15	0.0005	0.0004	0.50	0.38
	<i>N</i> = 10,000	<u>0.100</u>	0.092	NC	0.052	0.038	0.040	<u>0.026</u>	0.025	0.00005	—	0.50	—

Underlined numbers indicate where the diffusion approximation is outside the 95% confidence interval of the simulations. The diffusion approximations within boxes were outside the 95% confidence interval for most *N*. NC, the diffusion approximation did not converge to a numerical solution.

<sup>a</sup>Diffusion approximation using Equation 5.

<sup>b</sup>Mean of 10,000 stochastic simulations.

<sup>c</sup>Diffusion approximation using Equation 6; time is measured in generations/4*N*.

<sup>d</sup>Mean of 10,000 stochastic simulations; time is measured in generations/4*N*.

<sup>e</sup>*sv* = 0.1, *sf* = 0, *sm* = 0.

<sup>f</sup>*sv* = 0, *sf* = 0.1, *sm* = 0.

<sup>g</sup>*sv* = 0, *sf* = 0, *sm* = 0.1.



vantageous alleles more often than others may have an evolutionary advantage, and this may influence the evolution of plant life history characteristics such as selfing rate of the species. Depending on the dominance relationship of new advantageous alleles and the mode of selection, it may be an advantage to be either a selfing or an outcrossing species, and in two cases, a dominant allele under fecundity selection and a recessive allele under male sexual selection, it may be evolutionarily beneficial to have a mixed mating strategy. Likewise, it may be evolutionarily important to fix advantageous alleles quickly, and for most parameter value combinations the expected fixation time decreased with selfing rate, but interestingly, for an advantageous allele under male sexual selection, the smallest fixation time may occur at an intermediary selfing rate. It is important to note that such an evolutionary scenario depends on a group selection mechanism, which has been argued to be a relatively weak evolutionary force (Lewontin 1970). The above-mentioned effects of the fixation process of advantageous alleles have to be complemented with the intensely studied effects of deleterious alleles (Charlesworth *et al.* 1990; Uyenoyama and Waller 1991; Damgaard 1996), as well as a number of ecological effects (Holsinger 1992), to understand the evolution of mating systems in plants.

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