Inbreeding Depression Due to Overdominance in Partially Self-Fertilizing Plant Populations

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ABSTRACT

The effect of the rate of partial self-fertilization and viability selection on the magnitude of inbreeding depression was investigated for the overdominance genetic model. The influence of these factors was determined for populations with equilibrium genotypic frequencies. Inbreeding depression was measured as the normalized disadvantage in mean viability of selfed progeny as compared to outcrossed progeny. When caused by symmetric homozygous disadvantage at a single locus it is shown always to be less than one-third. Moreover, for fixed rates of self-fertilization, its maximum value is found at intermediate levels of homozygous disadvantage. As the rate of self-fertilization increases, inbreeding depression increases and the homozygote viability that results in maximum depression tends toward one-half the heterozygote viability. Symmetric selection against homozygotes at multiple loci can lead to substantially higher values than selection at a single-locus. As the number of independent loci involved increases, inbreeding depression can reach high levels even though the selfing rate is low. Viability distributions for progenies produced from both random mating and self-fertilization were derived for the case of symmetric selection at independently assorting multiple loci. Distributions of viabilities in progenies resulting from mixtures of selfing and outcrossing were shown to be bimodal when inbreeding depression is high.

INBRED offspring often have a disadvantage in fitness when compared with progeny from outcrossing. This phenomenon, known as inbreeding depression, is especially common in predominantly outcrossing plant species. Two genetic models have been proposed to account for it: (a) a model in which recessive or partially dominant lethal or sublethal alleles are held in equilibrium by selection-mutation balance (*e.g.*, see LANDE and SCHEMSKE 1985) and (b) the overdominance model. A review of results for the support of each of these models has recently been presented by CHARLESWORTH and CHARLESWORTH (1987).

In this paper we investigate the effects of partial self-fertilization and overdominance on inbreeding depression in natural populations. Inbreeding depression occurs because progeny produced by self-fertilization have higher homozygote frequencies than outcrossed progeny and selection against homozygotes thus results in a viability disadvantage for the selfed offspring.

A number of population genetic models include inbreeding depression as a force that balances reproductive factors favoring inbreeding. For example, in the work of LLOYD (1979) and HOLSINGER, FELDMAN and CHRISTIANSEN (1984), inbreeding depression was viewed as a force opposing the evolution of increased selfing. CHARLESWORTH and CHARLESWORTH (1979) investigated the antagonistic effect of inbreeding depression on the invasion of self-fertility alleles in self-incompatibility systems. CHARLESWORTH (1985) also described the impact of inbreeding depression on the evolution of particular sexual systems such as gynodioecy and androdioecy. In all of these investigations, inbreeding depression is treated as a fixed quantity that measures the relative viability disadvantage for inbred progeny. CAMPBELL (1986), however, correctly argues that, because of its sensitivity to genetic structure, inbreeding depression is not a useful concept for addressing questions about evolution of mating behavior. This was confirmed by CHARLESWORTH and CHARLESWORTH (1987) who presented examples documenting the effect of both selection and self-fertilization on inbreeding depression.

The effects of selection and mating parameters on inbreeding depression are quite complex. Inbreeding depression, for example, is not a monotone function of selection intensity against homozygotes. This can be illustrated for a single locus with two alleles by considering extreme selection intensities. If the homozygote disadvantage is very small, progeny produced by self-fertilization will have only a slight disadvantage compared with outcrossed progeny and the resulting inbreeding depression is expected to be

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small. If, on the other hand, the homozygote disadvantage is extremely large, almost all matings, whether by selfing or outcrossing, will involve heterozygotes. As a consequence, genotypic proportions will be similar under both types of mating, namely approximately 25% for each of the homozygotes and 50% for the heterozygotes. Because genotypic proportions for the inbred and outcrossed progenies are similar, inbreeding depression is again expected to be small. Since the depression is expected to be low under both high and low levels of homozygote disadvantage, it seems likely that it reaches a maximum at an intermediate level of homozygote disadvantage.

Throughout this paper we assume that the selfing rate is uniform for all genotypes and begin by investigating overdominance in viability at a single gene locus. Equilibrium properties under these conditions were first considered by HAYMAN (1953) and further elaborated by others (*e.g.*, WORKMAN and JAIN 1966; KIMURA and OHTA 1971; ZIEHE 1982). We determine mean viabilities for both selfed and outcrossed progenies as well as the distribution of viabilities within each of the two types of progenies. These mean viabilities depend on genotypic frequencies, which may change over generations and consequently, the amount of inbreeding depression also may vary. Here we report results on inbreeding depression for equilibrium genotypic frequencies.

Inbreeding depression is rarely due to effects expressed at a single gene locus, but is usually the combined result of effects at a number of loci. To study the effect of multiple loci on the difference in viabilities for selfed and outcrossed progeny, fitness effects at more than one ontogenetic stage in the life cycle are investigated. To avoid further complications, viability effects at any one stage are considered to be controlled by a single-locus acting independently of loci controlling effects at previous stages.

THE MODEL

We assume an infinite population of diploid cosexual plants that reproduce in nonoverlapping generations. We begin by considering a single autosomal gene locus with two alleles, A_1 and A_2, at which viability selection acts between the zygotic and adult stage of the life cycle. Viability selection coefficients are designated v_{11}, v_{12}, and v_{22} for the unordered genotypes A_1A_1, A_1A_2, and A_2A_2.

Reproduction is considered to follow the mixed mating model. A proportion σ of the ovules is reserved a priori to be fertilized by pollen from the individual that produced the ovules whereas the remaining proportion is fertilized randomly from the common pollen pool of the population. This is the prior selfing model discussed by LLOYD (1979). Genotypes are assumed to have identical ovule production as well as identical contributions to the common pollen pool.

Mean viabilities under symmetrical homozygote disadvantage: Inbreeding depression results from viability differences between selfed and outcrossed offspring. We first restrict consideration to identical homozygote viabilities. If the viability of the heterozygote is assigned a value of 1 ($v_{12} = 1$) and the disadvantage of the homozygotes in viability as compared with the heterozygote is denoted by s, then $v_{11} = v_{22} = 1 - s$. The values $s = 0$ and $s = 1$ represent analytically trivial cases for which mean viabilities of selfed and outcrossed progenies are identical. We thus assume $0 < s < 1$. At $\sigma = 0$, no selfed progenies are produced and at $\sigma = 1$ there are no outcrossed progeny, thus in either case comparisons between mean viabilities of selfed and outcrossed progenies are not possible. Hence we also assume $0 < \sigma < 1$. For incomplete selfing the assumption of symmetrical selection coefficients, unlike the case for strongly asymmetrical selection, guarantees that the diallelic polymorphism will be maintained in the population. If the rate of self-fertilization is large, asymmetrical homozygote viabilities ($v_{11} \neq v_{22}$) may lead to fixation of one of the alleles and to the absence of polymorphic equilibria (KIMURA and OHTA 1971; ZIEHE 1982).

For the case of symmetrical viabilities, zygotic genotypic frequencies converge to a globally stable polymorphic equilibrium with allele frequency equal to 1/2 (ZIEHE 1982). The zygotic heterozygote equilibrium frequency $\hat{P}^z_{12}$ (z indicates the zygotic stage and ($\hat{\ }$) the equilibrium property) has also been shown to be

$$\hat{P}^z_{12} = \Big[d + \sigma - 2 + \sqrt{(d + \sigma - 2)^2 + 8(1 - \sigma)d}\Big]/(4d), \quad (1)$$

where $d = s/(1 - s)$ (ZIEHE 1982). Each homozygote genotype consequently occurs at an equilibrium frequency of 0.5 $(1 - \hat{P}^z_{12})$.

After selection, the adult population has a relative heterozygote frequency of

$$\hat{P}^a_{12} = \hat{P}^z_{12}/[1 - s(1 - \hat{P}^z_{12})], \quad (2)$$

which, due to the heterozygote advantage, is always larger than $\hat{P}^z_{12}$.

At equilibrium, genotypic frequencies within the selfed offspring are found to be $\hat{P}^a_{12}/2$ for heterozygotes and $1 - \hat{P}^a_{12}/2$ for combined homozygotes. Consequently, the mean viability of the selfed offspring, $\bar{v}_s$, is:

$$\begin{aligned}\bar{v}_s &= \hat{P}^a_{12}/2 + (1 - s)(1 - \hat{P}^a_{12}/2) \\ &= 1 - s(1 - \hat{P}^a_{12}/2).\end{aligned} \quad (3)$$

During cross-fertilization, alleles associate independently in the formation of zygotes. Hence, genotypic frequencies within cross-fertilized progenies are in Hardy-Weinberg proportions. Since the equilibrium allele frequencies are 1/2, $\hat{P}^z_{11} = \hat{P}^z_{22} = 1/4$ and $\hat{P}^z_{12} = 1/2$ at the globally stable equilibrium. It follows then that mean viability of cross-fertilized zygotes, $\bar{v}_c$, is simply

$$\bar{v}_c = 1/2 + (1 - s)/2 = 1 - s/2. \tag{4}$$

Thus with $0 < s < 1$ and $0 < \sigma < 1$ $\bar{v}_s$ is always less than $\bar{v}_c$. Since allele frequencies are 1/2, $\bar{v}_c$ does not depend on the rate of self-fertilization. If the selective disadvantage of the different homozygotes is not identical, however, this will change.

Single-locus selection: Inbreeding depression has generally been defined as the relative viability disadvantage of inbred offspring compared with those resulting from outcrossing (*e.g.*, see LANDE and SCHEMSKE 1985; CHARLESWORTH and CHARLESWORTH 1987). Denoting inbreeding depression by δ and using this definition we obtain

$$\delta = 1 - \bar{v}_s/\bar{v}_c. \tag{5}$$

$\delta = 0$ indicates the absence of differences in viabilities between selfed and outcrossed progeny, $\delta = 1$ represents the largest meaningful value for inbreeding depression and no survival of selfed progeny.

The amount of inbreeding depression observed for the globally attractive, polymorphic equilibrium is illustrated in Figure 1. Obviously δ strongly depends on the selective disadvantage s of the homozygotes as well as the rate σ of self-fertilization. For the cases of either extremely strong or very slight selection against homozygotes, the expectation that inbreeding depression becomes small is confirmed. Clearly the greatest inbreeding depression occurs at an intermediate selection intensity.

The functional dependence of δ on σ and s is too complex to obtain a simple expression for the value of s that maximizes δ. It can be seen, however, that the value of s that produces the maximum δ is shifted toward 1/2 as σ increases. It is nevertheless possible to derive an upper bound for the amount of inbreeding depression due to single-locus selection.

Consider the expression for $\hat{P}^z_{12}$ given in (1). As a function of σ, it is monotonically decreasing. Evaluating this expression at extremely large amounts of self-fertilization (σ close to 1), we immediately see that $\hat{P}^z_{12} > 0$ if $0 < s \leq 1/2$ and $\hat{P}^z_{12} > (2s - 1)/(2s)$ if $1/2 < s < 1$. For the frequencies in the adult stage, the comparable expressions are $\hat{P}^a_{12} > 0$ for $0 < s \leq 1/2$ and $\hat{P}^a_{12} > (2s - 1)/s$ for $1/2 < s < 1$. With these lower bounds for $\hat{P}^a_{12}$, it is clear from Equation 3 that $\bar{v}_s$ cannot be arbitrarily small and

$$\bar{v}_s \begin{cases} > 1 - s & \text{if} \quad 0 < s \leq 1/2 \\ > 1/2 & \text{if} \quad 1 > s > 1/2, \end{cases} \tag{6}$$

yielding

$$\frac{\bar{v}_s}{\bar{v}_c} \begin{cases} > 2(1 - s)/(2 - s) & \text{if} \quad 0 < s \leq 1/2 \\ > 1/(2 - s) & \text{if} \quad 1 > s > 1/2. \end{cases} \tag{7}$$

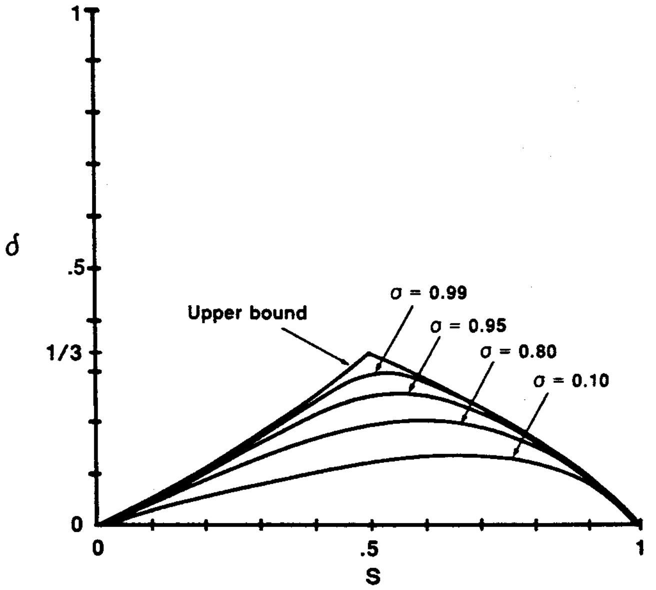

FIGURE 1.—Equilibrium inbreeding depression (δ) for various rates of selfing (σ) with the upper limit for single-locus symmetrical selection.

These latter functions determine lower bounds for $\bar{v}_s/\bar{v}_c$. Corresponding upper bounds for inbreeding depression δ, are illustrated in Figure 1. The above derived lower bounds for $\bar{v}_s/\bar{v}_c$ have a minimum value at $s = 1/2$. Consequently, $\bar{v}_s/\bar{v}_c$ always exceeds two-thirds and the inbreeding depression δ must be less than one-third, *i.e.*, $\delta < 1/3$.

Selection at *N* independent loci: Under multiple-locus selection and mixed mating, the genotypic frequencies have complicated dynamical behavior (HEDRICK 1985). It is therefore important to examine this case, rather than to assume that the system behaves in the same way as for a single locus, and thus to determine how additional loci affect the overall level of inbreeding depression. We restrict our consideration to the particular case of symmetrical selection acting on a different gene locus at each ontogenetic stage in the life cycle with all such loci being unlinked. For selection models of this type, survival probabilities for multiple-locus genotypes are products of the conditional probabilities for survival at each ontogenetic stage given survival at the previous stage (*i.e.*, the single-locus viability parameters).

We again assume that both homozygotic genotypes at a locus have the same viability disadvantage and that the viability selection parameters are identical for all ontogenetic stages and thus for all gene loci. We consider a number of gene loci, N, and again $1 - s$ and 1 are the single-locus viability parameters for homozygotes and heterozygotes, respectively. With this type of symmetry in the selection parameters and with products of single-locus equilibrium frequencies as values for initial genotypic frequencies, it is possible to restrict the description of genotypic dynamics to transition equations for frequencies of individuals with specific numbers of heterozygous loci. These transition equations can be used to numerically determine polymorphic multiple-locus equilibria.

Let the frequency of adults that are heterozygous at exactly n loci be represented by $P^a(n)$ where $0 \leq n \leq N$ and

$$\sum_{n=1}^{N} P^a(n) = 1.$$

In the subsequent generation, the frequency of *selfed* progeny heterozygous at i loci which arise from adults heterozygous at n loci is $\binom{n}{i} P^a(n)/2^n$. Therefore the total frequency of *selfed* progeny heterozygous at i loci is

$$P_s'(i) = \sum_{n=i}^{N} \binom{n}{i} \left(\frac{1}{2}\right)^n P^a(n). \tag{8}$$

We assume that initial adult allele frequencies are one-half at each locus. Thus, the frequency of heterozygotes at each locus equals 1/2 in the *outcrossed* progeny. With free recombination, multiple-locus genotypic frequencies within randomly outcrossed progenies are products of the single-locus genotypic frequencies. As a result, the frequency of *outcrossed* progeny in the next generation that are heterozygous at exactly i loci can be expressed as

$$P_c'(i) = \binom{N}{i} \left(\frac{1}{2}\right)^N. \tag{9}$$

Frequencies of adults heterozygous at n loci in the next generation are obtained using the corresponding frequencies in the selfed and outcrossed progenies and the viability parameters. These adult frequencies, consequently, are given by

$$P^{a\prime}(n) = (1-s)^{N-n}[(1-\sigma)P_c'(n) + \sigma P_s'(n)]/\bar{v}'(N) \tag{10}$$

where $\bar{v}'(N)$ indicates mean viability for N loci and is computed over all progenies. The overall mean viability in each generation is a weighted average of the mean viabilities for the selfed and outcrossed progenies. Thus

$$\bar{v}(N) = \sigma\bar{v}_s(N) + (1-\sigma)\bar{v}_c(N) \tag{11}$$

where $\bar{v}_s(N)$ represents mean viability of the selfed progeny and $\bar{v}_c(N)$ represents the corresponding mean viability for the outcrossed progeny. The mean viability for the selfed progeny can be expressed as

$$\bar{v}_s'(N) = \sum_{i=0}^{N} (1-s)^{N-i} P_s'(i) \tag{12}$$

which upon substitution of the expression in (8) reduces to

$$\bar{v}_s'(N) = \sum_{n=0}^{N} (1-s)^{N-n}[1-s/2]^n P^a(n). \tag{13}$$

Likewise for outcrossed progeny,

$$\bar{v}_c'(N) = \sum_{i=0}^{N} (1-s)^{N-i} P_c'(i) \tag{14}$$

which simplifies to

$$\bar{v}_c'(N) = [1-s/2]^N \tag{15}$$

after substitution of the equation given in (9) for $P_c'(i)$.

Inbreeding depression resulting from the effects produced by multiple loci depends upon the difference between the mean viabilities for outcrossed and self progenies. Therefore, an appropriate measure for inbreeding depression produced by N loci is

$$\delta(N) = 1 - [\bar{v}_s(N)/\bar{v}_c(N)]. \tag{16}$$

Mean viabilities and inbreeding depression values were now evaluated for equilibrium conditions. Equilibrium frequencies for specific numbers of heterozygous loci in adult individuals $P^a(n)$ were determined by numerical iteration using the above transition equations and initial values computed as products of the single-locus equilibrium genotypic frequencies. In all of our iteration series, rapid convergence to equilibrium was observed. Changes in frequencies were relatively small after 50 generations ($|P^{a\prime}(n) - P^a(n)| < 10^{-4}$). Frequencies obtained after 500 generations were assumed to be sufficiently close to equilibrium values and were used to determine equilibrium mean viabilities and amounts of inbreeding depression. Identical inbreeding depression results have been obtained for this model by D. CHARLESWORTH (personal communication) using different methods.

The effect of different numbers of gene loci on inbreeding depression is illustrated in Figure 2 for predominantly outcrossing ($\sigma = 0.10$) and predominantly self-fertilizing ($\sigma = 0.95$) populations. It is clear from Figure 2 that high levels of inbreeding depression can be reached if several loci are involved. For a predominantly outcrossing species with slight overdominance effects, however, a substantial number of loci is required to obtain pronounced inbreeding depression.

Distribution of viability among selfed and outcrossed progeny: An important consideration for investigating the evolution of selfing types is the distribution of selfed and outcrossed offspring over the range of different viabilities. Like the corresponding mean viabilities, these distributions will generally change during the establishment of mutations that affect the selfing rate. We restrict our considerations

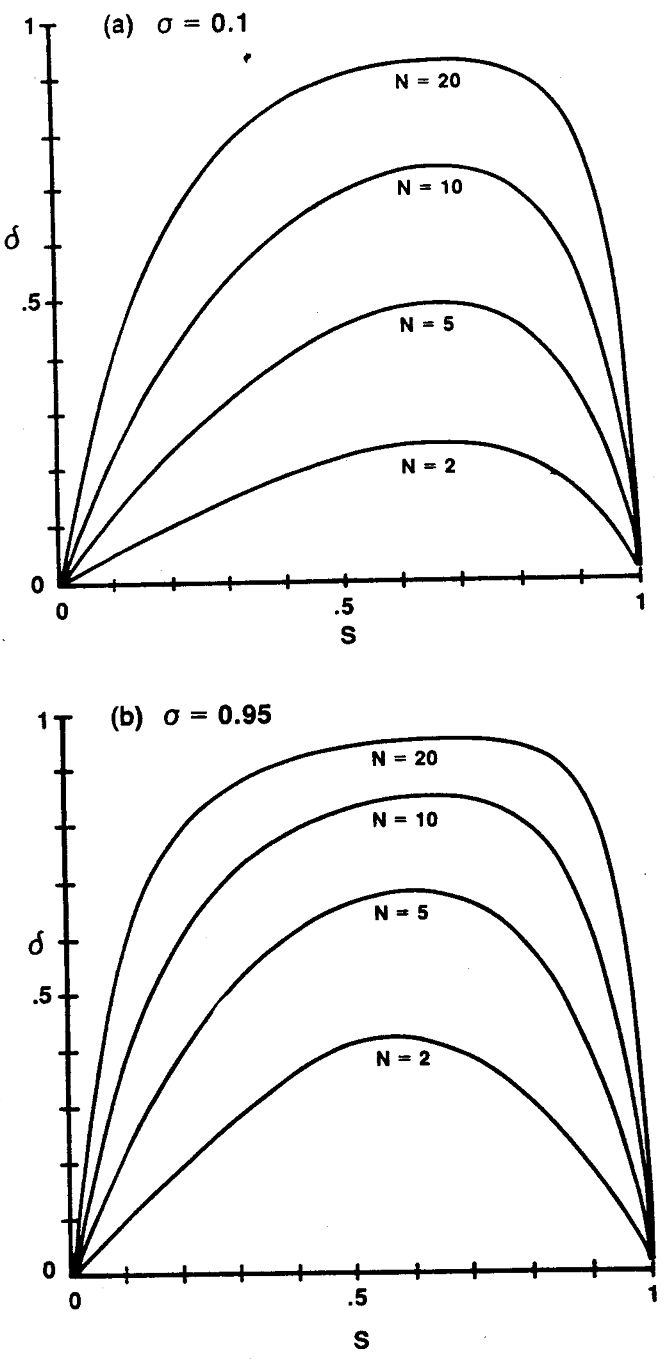

FIGURE 2.—Equilibrium inbreeding depression (δ) due to viability selection at N independent loci. Viability disadvantage of homozygotes (s) is assumed to be uniform over loci. Inbreeding depression is shown (a) for a predominantly outcrossing population ($\sigma = 0.1$) and (b) for a predominantly self-fertilizing population ($\sigma = 0.95$).

to investigation of the viability distributions for polymorphic multiple-locus equilibria determined by the method described in the previous section. Of particular interest is again the difference between the distributions for selfed and outcrossed progeny and the influence of selfing rate and viability parameters on these distributions.

With the assumption of identical selection regimes for all loci affecting viability, the different viabilities for progeny are given by $(1-s)^{N-i}$ where i represents number of heterozygous loci and $0 \leq i \leq N$. Since $P_s(i)$ is the frequency of selfed progeny with i heterozygous loci in any one generation, it also represents the proportion of selfed progeny with viability $(1-s)^{N-i}$, and at the equilibrium we have $\Pr[v = (1-s)^{N-i}] = \hat{P}_s(i)$ for selfed progeny. The expression representing $\hat{P}_s(i)$ can be obtained from Equation 8. For outcrossed progeny, the probability of obtaining progeny with viability $(1-s)^{N-i}$ is given by $\hat{P}_c(i)$. The equation representing $\hat{P}_c(i)$ can be taken from (9).

Equilibrium probabilities for viabilities in the mixed set of selfed and outcrossed progenies are simply the weighted averages of the equilibrium probabilities for the selfed and outcrossed progenies. Probability of progeny occurring with viability $(1-s)^{N-i}$ in the mixed progeny set is

$$\Pr[v = (1-s)^{N-i}]$$
$$= \sigma\left[\sum_{n=i}^{N} \binom{n}{i}\left(\frac{1}{2}\right)^{n} \hat{P}^{a}(n)\right] + (1-\sigma)\binom{N}{i}\left(\frac{1}{2}\right)^{N}. \quad (17)$$

Viability probability distributions in sets of mixed progenies may be unimodal or bimodal depending on differences between the means and variances of selfed and outcrossed progenies. Equilibrium probability distributions in selfed, outcrossed, and mixed progenies for viability effects at 20 loci and at low and intermediate rates of self-fertilization are illustrated in Figure 3.

Variances among viabilities within progenies can also be derived for these probability distributions. Here we consider only the equilibrium variances. For selfed progeny, assuming N loci,

$$\sigma_s^2 = \sum_{i=0}^{N} (1-s)^{2(N-i)} \quad (18)$$
$$\cdot\left(\sum_{n=i}^{N} \binom{n}{i}\left(\frac{1}{2}\right)^{n} \hat{P}^{a}(n)\right) - [\bar{v}_s(N)]^2$$

which reduces to

$$\sigma_s^2 = \sum_{n=0}^{N} \hat{P}^{a}(n)(1-s)^{2(N-n)}(1-s+s^2/2)^{n} - [\bar{v}_s(N)]^2. \quad (19)$$

Likewise, the variance among viabilities for the outcrossed progeny can be expressed as

$$\sigma_c^2 = \sum_{i=0}^{N} (1-s)^{2(N-i)} \binom{N}{i}\left(\frac{1}{2}\right)^{N} - [\bar{v}_c(N)]^2 \quad (20)$$

which reduces to

$$\sigma_c^2 = (1-s+s^2/2)^N - (1-s+s^2/4)^N. \quad (21)$$

In the distributions illustrated in Figure 3 it is apparent that $\sigma_c^2 > \sigma_s^2$.

Asymmetrical homozygote disadvantage: As pre-

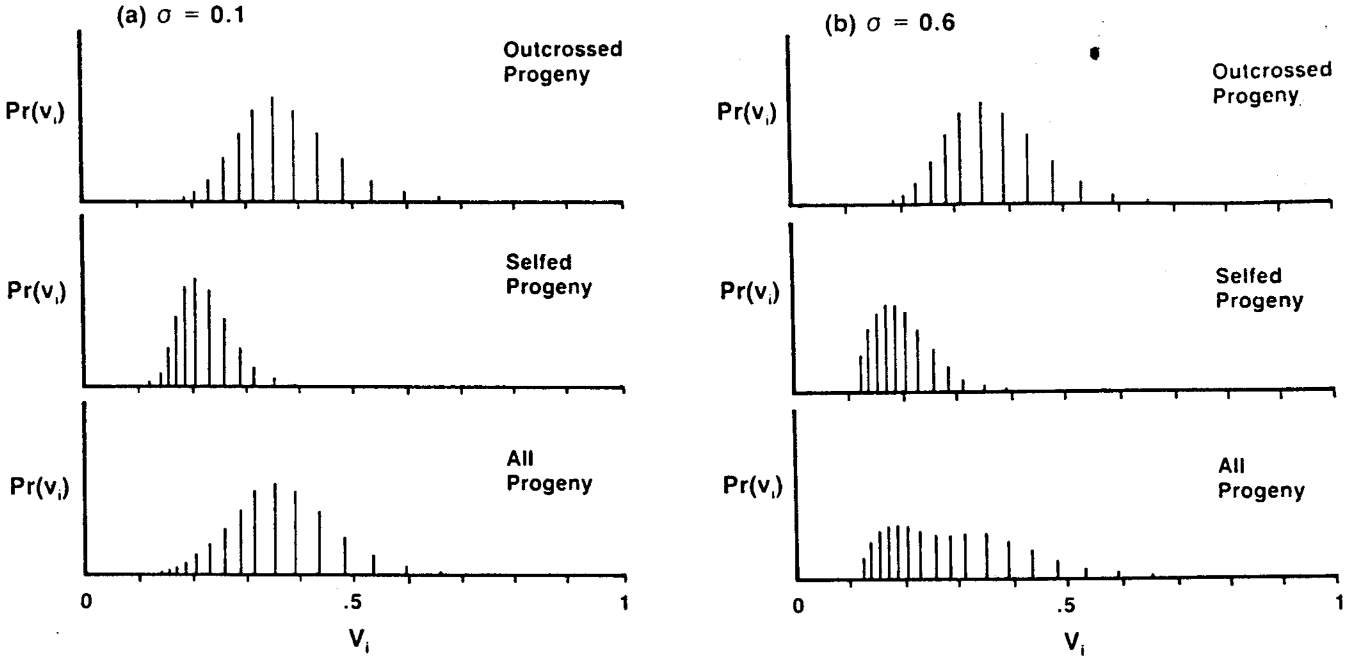

FIGURE 3.—Probability distributions for viability (v_i) in outcrossed, selfed, and mixed progenies. Distributions are for viabilities produced by a 10% per locus homozygous disadvantage ($s = 0.1$) at 20 loci. Distributions are shown for progenies generated (a) predominantly from outcrossing ($\sigma = 0.1$) and (b) intermediate selfing ($\sigma = 0.6$).

viously mentioned, under a regime of pronounced asymmetry in homozygote viability disadvantage and a sufficiently large selfing rate, the polymorphic equilibrium vanishes and fixation results from selection. It is of interest, however, to determine the amount of inbreeding depression within the asymmetrical polymorphic equilibria that do exist. These equilibria show allele frequencies different from 0.5. In this section, viabilities for the genotypes A_1A_1, A_1A_2, and A_2A_2 are represented by $1 - s_1$, 1, and $1 - s_2$. The equilibrium frequency is derived from the results of WORKMAN and JAIN (1966). We get an equilibrium fixation index $\hat{F}$ ($\hat{F} = 1 - \hat{P}^*_{12}/[2\hat{p}^*_1\hat{p}^*_2]$) which is the solution of a quadratic equation:

$$\hat{F} = [(2-\sigma)a + 1]/2 - \sqrt{[(2-\sigma)a + 1]^2/4 - \sigma a}, \qquad (22)$$

where $a = (s_1 + s_2 - 2s_1s_2)/(2s_1s_2)$. The equilibrium allele frequency of A_1 can be determined by

$$\hat{p}^*_1 = (s_2 - \hat{F}s_1)/[(1 - \hat{F})(s_1 + s_2)]. \qquad (23)$$

With $\hat{F}$ and $\hat{p}^*_1$ the genotypic frequency at equilibrium is easily reconstructed. The derivation of mean viabilities of selfed and outcrossed progeny and the determination of inbreeding depression follows in an analogous way as for the case of identical homozygote disadvantage. Some examples of inbreeding depression for these asymmetrical polymorphic equilibria are illustrated in Figure 4. It is clear from these illustrations that symmetrical selection is very effective in producing inbreeding depression. For those regimes we investigated, the highest levels of inbreeding depression for fixed selfing rates occurred for intermediate symmetrical selection against homozygotes. The reason for this result becomes evident when considered in the following context. With symmetrical homozygote disadvantage a relatively high frequency of heterozygotes occurs at genotypic equilibrium. As a result large differences in mean viabilities between selfed and outcrossed offspring are possible. As asymmetry increases, however, heterozygote frequency declines and equilibrium frequencies move towards fixation [see ZIEHE (1982) for a graphical representation of the equilibrium location in de Finetti diagrams]. Differences in genotypic frequencies for selfed and outcrossed progenies then become smaller and mean viabilities differ less than for the symmetric case. With selection for fixation at a particular locus and thus no polymorphic equilibrium, the contribution of this locus to inbreeding depression of course becomes zero.

DISCUSSION

The amount of inbreeding depression at genotypic frequency equilibrium has been shown to depend strongly on the magnitude of selection against the homozygotes. Maximum inbreeding depression for a fixed rate of selfing has also been demonstrated to occur at intermediate selection intensity. Moreover, as the rate of self-fertilization increases, the value of the homozygotic disadvantage that produces the maximum inbreeding depression is shifted from a high value, which indicates strong selection against homozygotes, toward a selection regime in which homozygotes have exactly half the viability of the heterozygotes. Hence, especially for predominantly self-fertilizing populations, selection with approximately half the heterozygote viability for the homozygotes gives the maximum amount of inbreeding depression due to single-locus overdominance. The amount of inbreeding depression, however, if due to single-locus selection, is always below one-third. Inbreeding depression may be even substantially smaller for populations that have a low selfing rate (*e.g.*, predominantly outcrossing populations) and that show only a few percent viability disadvantage for selfed progeny.

The amount of self-fertilization has a different effect on inbreeding depression depending upon whether it is the result of overdominance or of recessive deleterious alleles held in the population by mutation-selection balance. Under the latter model, LANDE and SCHEMSKE (1985) concluded that the amount of inbreeding depression decreases with an increasing rate of self-fertilization. With the overdominance model, however, our results confirm the conclusion of CHARLESWORTH and CHARLESWORTH (1987) that the amount of inbreeding depression increases with increasing self-fertilization provided that viability selection against homozygotes is sufficiently symmetrical. If, however, selection against homozygotes is asymmetrical, an increased rate of selfing may lead to fixation, which implies that such a locus no longer contributes to inbreeding depression. Hence, depending on the amount of asymmetry in homozygote disadvantage, inbreeding depression is either increased or decreased. From previous results about the maintenance of polymorphisms under selection and mixed mating, it is known that predominantly outcrossing species are less likely to lose polymorphisms than are inbreeding species because of small changes in either selection pressure or the selfing rate. Consequently, it is expected that a higher degree of selfing will probably cause higher inbreeding depression in predominantly outcrossing populations, whereas in predominantly self-fertilizing populations, a lower amount of inbreeding depression is likely to be observed unless selection at all loci is nearly symmetrical.

Inbreeding depression can easily be introduced into natural populations and then may evolve. If in a partially self-fertilizing population a polymorphism becomes established showing heterozygote superiority in viability, inbreeding depression has to simultaneously appear or be enhanced. The amount of change in inbreeding depression that will occur depends

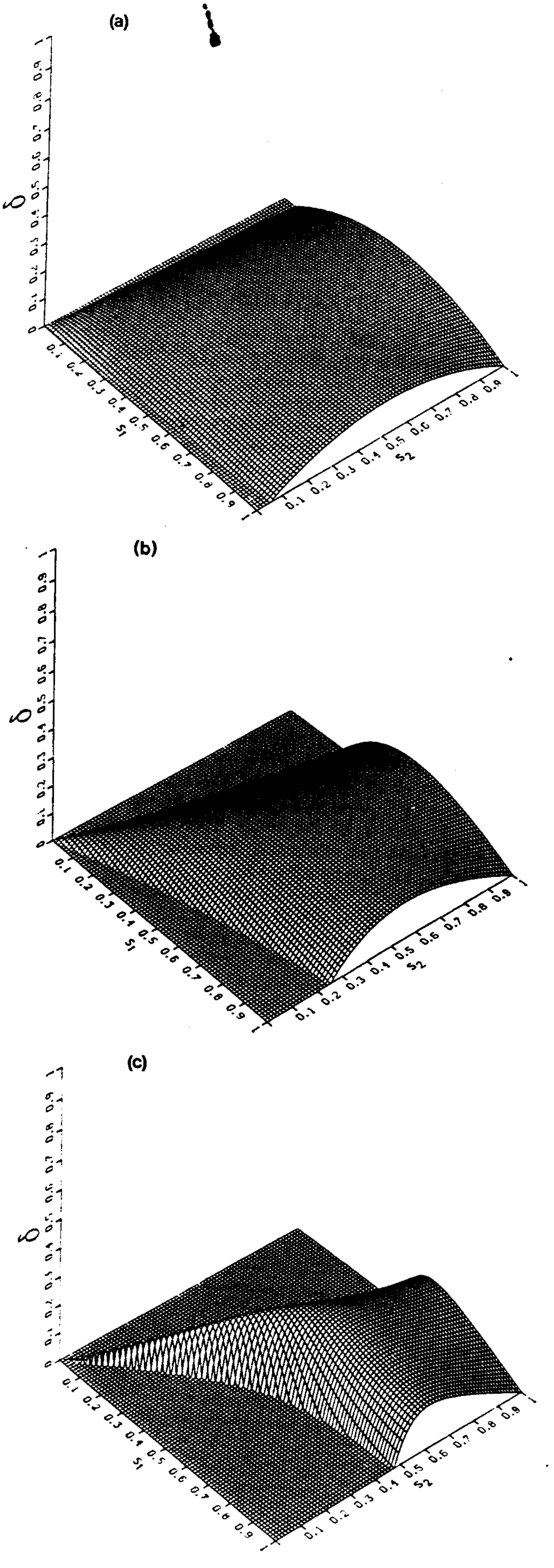

FIGURE 4.—Equilibrium inbreeding depression (δ) resulting from asymmetrical homozygous disadvantage (s_1, s_2) at a single-locus (a) for a predominantly outcrossing population ($\sigma = 0.10$), (b) for $\sigma = 0.50$, and (c) for a predominantly self-fertilizing population ($\sigma = 0.95$).

strongly on the amount of selection disadvantage for homozygotes.

Selection at multiple loci can lead to a substantially larger inbreeding depression than is possible for selection at a single-locus. Especially in predominantly outcrossing species, relatively large numbers of loci are required to obtain a substantial effect. With five loci and a selfing rate of 10%, an inbreeding depression of 50% is reached only for a small range of selection coefficients, $0.64 < s < 0.68$. With 10 loci and the same selfing rate, values of inbreeding depression greater than 50% are reached for a greater range of selection coefficients, $0.27 \leq s \leq 0.91$. Hence, an accumulation of inbreeding effects over several loci is indeed likely to lead to substantial amounts of inbreeding depression.

With overdominance as the cause of inbreeding depression, the mean population viability $\bar{v}(N)$, where $\bar{v}(N) = \sigma\bar{v}_s(N) + (1 - \sigma)\bar{v}_cN$, is expected to be less than the mean viability $\bar{v}_cN)$ of the outcrossed progeny. It has additionally been shown that substantial inbreeding depression requires that a large number of loci be involved in viability selection as well as sufficiently intermediate selection effects against homozygotes. This requirement, however, forces $\bar{v}_c(N)$ and consequently $\bar{v}(N)$ to decrease. Hence, a high level of inbreeding depression has to be associated with a relatively low population viability—a fact that may eventually help to differentiate between possible causes of inbreeding depression.

Progenies in partly self-fertilizing populations vary substantially in viability. Differences in the distribution of viabilities in selfed and outcrossed progenies have been characterized by differences in the genotypic frequencies for these two groups. The inbreeding depression measure (δ) only quantifies the difference in mean viability between selfed and outcrossed progenies. If inbreeding depression is large, it has been demonstrated that viability distributions of all progeny can be bimodal or even multimodal, with the lower viabilities occurring mainly in the selfed progenies.

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