Short-Term Loss of Neutral Alleles in Small-Population Breeding*)

By G. Namkoong and J. H. Roberds**)

(Received 4th August 1980)

Summary

Selecting on a quantitatively inherited trait affects the probability of loss of linked neutral alleles. The loss of such alleless in small population breeding is affected by the selection intensity, heritability, and linkage with the quantitative gene loci. Early generation losses are most seriously increased under linkage disequilibrium, but the effects are quickly dissipated by moderate recombination rates. Increased population sizes can also diminish these effects of selection.

Key words: Linkage, Selection, Breeding, Quantitative Inheritance

Zusammenfassung

Die Selektion auf ein quantitativ ererbtes Merkmal beeinträchtigt die Wahrscheinlichkeit des Verlustes verknüpfter, neutraler Allele. Der Verlust solcher Allele in kleinen Züchtungspopulationen wird durch Selektionsintensität, Heritabilität und die Verknüpfung mit quantitativen Genloci beeinflußt. Frühe Generationsverluste steigen durch das Ungleichgewicht der Verknüpfung stark an, aber die Effekte sind schnell durch gemäßigte Rekombinationsraten zerstreut. Erhöhte Populationsgrößen können auch diese Selektionseffekte vermindern.

Introduction

Recurrent selection programs often require shifts in selection objectives as the economic or environmental milieu changes. This is likely for trees with long generation intervals. It is therefore important to preserve allele variation in traits that may have value in the future while selecting for other traits of present importance. In small population breeding, the problem is particularly acute if the alleles to be favored in the future occur most often with alleles at other loci which are presently disfavored. We examine the possibilities of loss of alleles which have no initial selective value but which are negatively correlated in frequency with selected alleles at other loci. We consider a locus (locus A) with alleles that affect adaptability to future environmental stress, but which have no effect in present environments. This locus is considered to be linked to loci which affect a trait, such as growth, which is being improved by truncation selection.

For alleles at an initially neutral locus (locus A), associated with alleles at other loci, under present selection, changes in frequency and probabilities of fixation are dependent on population size, epistasis, and the degree of association between locus A and other loci. The general behavior of two loci with selection in finite populations has been studied by Karlin and McGregor (1968). Without epistasis and at linkage equilibrium, the theory of neutral genes is adequate. In this article, we examine breeding alternatives when populations are initially in disequilibrium due to sampling or prior selection. If the disequilibrium is such that a positive correlation exists between the trait under selection and the locus of interest, the loss of A alleles of future value will be less than with linkage equilibrium, and loss probabilities are not of great concern to the breeder. However, if the disequilibrium is such that an allele of future value at locus A is negatively correlated with the trait of present value, its fate is of major concern to the breeder.

Selection Model

To examine the fate of unfortunately associated alleles in small, random mating populations, the alleles of locus A are assumed to have no direct selection value, but other linked loci are assumed to affect a quantitatively inherited trait upon which truncation selection is exercised. Such a a model is appropriate for tree breeding programs in which truncation selection is undertaken in present environments to improve quantitative traits such as growth. Selection on the basis of individual merit is envisioned as being among individuals produced by random mating trees selected in the previous generation. The zygotes of locus A are assumed to be initially associated with alleles at the other loci which endow the zygotes with normally distributed selection values. Thus, each zygotic state has a different mean but the same variance. When truncation selection is applied to the quantitatively inherited trait, the allele of interest is then selected against. Therefore, the effect of selection on locus A is diminished to the extent that this initial effect of linked loci is reduced by recombination.

Under this model, the locus of interest has two alleles (A, a) which have no current selection value but which take on pseudo-selective value due to initial linkage disequilibrium with many other loci. These other loci have individually small but cumulatively large selective values. The effects of environmental variations and variations at other loci are assumed to produce a normal distribution of values with constant variance. The disequilibria are assumed to have small individual effects, but sufficient net cumulative effect for the three genotypes (AA, Aa, aa) to have different means.

Theory

We examine the expected changes at the A locus as they are influenced by selection on an associated quantitative trait. Selection is assumed to affect gene frequencies at loci affecting the quantitative trait according to Griffing's (1960) model. We examine the effects of initial disequilibrium between locus A and one of these other loci exemplified by (locus B) and extend the results to multiple "B" loci as they are expected to behave under quantitative inheritance.

If allele B is favored by selection on the quantitative trait, its expected advance in frequency is a function of its frequency, its average effect, and the per locus selection intensity. Considering only the pairwise disequilibrium

*) Joint contribution of the Department of Genetics, North Carolina Agricultural Experiment Station, Raleigh, North Carolina, and the Southeastern Forest Experiment Station. Paper No. 5662 of the Journal Series.

**) Research Geneticists Forest Service, U. S. Department of Agriculture, and North Carolina State University, Raleigh, North Carolina.

with the A locus to be significant, the effect of the changes at the B loci on the disequilibrium can be derived. Consider that the frequency of allele A (q_A) is changed by the amount δ which is apportioned among the gametes AB and Ab in proportion to the frequency of the alleles at the B locus, and the frequency of the alleles of the locus (q_B) is changed by an amount ε. If the four initial genetic frequencies f_{AB}, f_{Ab}, f_{aB}, f_{ab} are in linkage disequilibrium $D = f_{AB} f_{ab} - f_{Ab} f_{aB}$, then the gametic frequencies in the next generation can be written as in *Formula 1:*

$$f'_{AB} = f_{AB} - rD + \delta q_B + \varepsilon/2$$
$$f'_{Ab} = f_{Ab} + rD + \delta q_b - \varepsilon/2$$
$$f'_{aB} = f_{aB} + rD - \delta q_B + \varepsilon/2$$
$$f'_{ab} = f_{ab} - rD - \delta q_b - \varepsilon/2,$$

where r is the recombination fraction.
The new disequilibrium is then (See *Formula 2):*

$$D' = f'_{AB} f'_{ab} - f'_{Ab} f'_{aB} = (1-r) D - \varepsilon(q_A - q_a)/2 - \delta\varepsilon.$$

The average pairwise disequilibrium between the A locus and each of many other "B" loci is thus the original D less the portion of disequilibrium dissipated by recombination plus an average remainder term for each "B" locus which is dependent on changes in q_B. The expected value of the remainder is small since it is the product of small per locus selection intensities, gene frequencies, and average affects. ε is directly affected by selection and δ is affected indirectly through the disequilibrium. The terms involving ε and δ are therefore small and we hereafter ignore this bias.

If the above approximations are valid, it can also be shown that selection has little effect on average effects associated by linkage with the A locus. Taking a measure of genotypic value χ_2 for BB, χ_1 for Bb and χ_0 for bb, the genetic values of individuals with the AB gamete can be defined as in *Formula 3:*

$$\bar{\chi}_{AB} = \left[\frac{2f_{AB}}{AB}\chi_{AB} + \frac{f_{AB}}{Ab}\chi_{AB} + \frac{f_{AB}}{aB}\chi_{AB} + \frac{f_{AB}}{ab}\chi_{AB} \right] \Big/ 2f_{AB}$$
$$= \left[\left(\frac{2f_{AB}}{AB} + \frac{f_{AB}}{aB} \right)\chi_2 + \left(\frac{f_{AB}}{Ab} + \frac{f_{AB}}{ab} \right)\chi_1 \right] \Big/ 2f_{AB}$$

Assuming random genetic combinations and hence *(Form. 4):*

$$f_{\frac{AB}{AB}} = f_{AB} \cdot f_{AB}, \quad f_{\frac{AB}{aB}} = 2f_{AB} \cdot f_{aB},$$
$$f_{\frac{AB}{Ab}} = 2f_{AB} \cdot f_{Ab}, \quad f_{\frac{AB}{ab}} = 2f_{AB} \cdot f_{ab}.$$

Then since (see *Form. 5):*

$$\chi_{\frac{AB}{AB}} = \chi_{\frac{AB}{aB}} = \chi_{\frac{aB}{aB}} = \chi_2, \quad \chi_{\frac{AB}{ab}} = \chi_{\frac{aB}{ab}} = \chi_{\frac{AB}{Ab}} = \chi_{\frac{aB}{Ab}} = \chi_1,$$
$$\chi_{\frac{Ab}{Ab}} = \chi_{\frac{Ab}{ab}} = \chi_{\frac{ab}{ab}} = \chi_0,$$

the gametic values can be expressed as in *Form 6.*

$$\bar{\chi}_{AB} = (f_{AB} + f_{aB})\chi_2 + (f_{Ab} + f_{ab})\chi_1$$
$$\bar{\chi}_{AB} = q_B \chi_2 + q_b \chi_1.$$

We define an average effect of alleles at the A locus under this model as in *Form. 7.*

$$\alpha_A^{[0]} = (f_{AB} \bar{\chi}_{AB} + f_{Ab} \bar{\chi}_{Ab})/q_A^{[0]}$$
$$\alpha_a^{[0]} = (f_{aB} \bar{\chi}_{aB} + f_{ab} \bar{\chi}_{ab})/q_a^{[0]}$$

Since the B locus is in Hardy-Weinberg equilibrium in the initial generation, (see *Form. 8):*

$$(q_B^{[0]})^2 \chi_2 + 2q_B^{[0]} q_b^{[0]} \chi_1 + (q_b^{[0]})^2 \chi_0 = 0$$

and these average effects can be expressed as in *Form 9.*

$$\alpha_A^{[0]} = D^{[0]} \{q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)\}/q_A^{[0]}$$
$$\alpha_a^{[0]} = -D^{[0]} \{(q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)\}/q_a^{[0]}$$

where the subscript [0] refers to the generation 0.

It can also be derived that (see *Form. 10):*

$$\alpha_A^{[1]} = \{f_{AB}^{[1]} \bar{\chi}_{AB} + f_{Ab}^{[1]} \bar{\chi}_{Ab}\}/q_A^{[1]}$$
$$= D^{[1]} \{q_B^{[1]} (\chi_2 - \chi_1) + q_b^{[1]} (\chi_1 - \chi_0)\}/q_A^{[1]}$$
$$+ (q_B^{[1]})^2 \chi_2 + 2q_B^{[1]} q_b^{[1]} \chi_1 + (q_b^{[1]})^2 \chi_0.$$

Making substitutions for gene frequencies and linkage disequilibrium in terms of values in the previous generation (see *Form. 11):*

$$\alpha_A^{[1]} = \{(1-r) D^{[0]} [q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)]$$
$$+ \varepsilon(1-r) D^{[0]} (\chi_2 - 2\chi_1 + \chi_0)$$
$$+ \varepsilon/2 [q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)] (1 + 2q_A^{[0]}) + \frac{\varepsilon^2}{2} (\chi_2 - 2\chi_1 + \chi_0)$$
$$+ \delta\varepsilon [q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)]\} \div q_A^{[1]}.$$

In the expression that follows we ignore the products containing ε and take $\alpha_A^{[1]}$ to be (see *Form. 12):*

$$\alpha_A^{[1]} = (1-r) D^{[0]} [q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)]/q_A^{[1]}.$$

There are now two cases to determine: (see *Form. 13):*

(1) If $q_A^{[0]} = q_A^{[1]}$, then $\alpha_A^{[1]} = (1-r) \alpha_A^{[0]}$
(2) but if $q_A^{[0]} \neq q_A^{[1]}$, then $\alpha_A^{[1]} = (1-r) \alpha_A^{[0]} q_A^{[0]}/q_A^{[1]}$.

In the latter case, however, to determine the relationship between α effects when gene frequency changes, consider the average effect of the A allele defined in terms of the gene frequency in the initial generation, where i indicates the generation number. Thus, (see *Form. 14):*

$\beta_A^{[0]} = \alpha_A^{[0]}$, $\beta_a^{[0]} = \alpha_a^{[0]}$ and
$\beta_A^{[1]} = \alpha_A^{[1]} q_A^{[1]}/q_A^{[0]} = (1-r) \alpha_A^{[0]}$; similarly,
$\beta_a^{[1]} = \alpha_a^{[1]} q_a^{[1]}/q_a^{[0]} = (1-r) \alpha_a^{[0]}$. For the nth generation

(see *Form. 15):*

$$\beta_A^{[n]} = \alpha_A^{[n]} q_A^{[n]}/q_A^{[0]} \text{ and } \beta_a^{[n]} = \alpha_a^{[n]} q_a^{[n]}/q_a^{[0]}.$$

Hence, for any change in gene frequency, we can predict the change in average effect on the basis of the initial gene frequency $q_A^{[0]}$. If C_A is defined as in *Form. 16* and *17:*

$C_A = \{q_B^{[0]} (\chi_2 - \chi_1) + q_b^{[0]} (\chi_1 - \chi_0)\}/q_A^{[0]}$, then from the definition of $\beta_A^{[1]}$ and $\alpha_A^{[1]}$,

$$\beta_A^{[1]} = (1-r) D^{[0]} C_A.$$

Similarly, see *Form. 18:*

$$\beta_a^{[1]} = -(1-r) D^{[0]} C_a \text{ where } C_a = C_A q_A^{[0]}/q_a^{[0]}.$$

For the nth generation see *Form. 19:*

$$\alpha_A^{[n]} = q_A^{[0]} \{\alpha_A^{[0]} - [1-(1-r)^n] D^{[0]} C_A\}/q_A^{[n]} \text{ and thus}$$
$$\beta_A^{[n]} = (1-r) D^{[n]} C_A.$$

Also, see *Form. 20:*

$$\alpha_a^{[n]} = q_a^{[0]} \{\alpha_a^{[0]} + [1-(1-r)^n] D^{[0]} C_a\}/q_a^{[n]} \text{ so}$$
$$\beta_a^{[n]} = -(1-r) D^{[n]} C_a.$$

The genotypic values change in each generation and the differences will eventually approach zero as D decays to zero. In a linear model for the mean of a genotypic distribution, with the alleles A_i and A_j, the mean of A_iA_j is $\mu + \alpha_i + \alpha_j + \delta_{ij}$ where μ is the general population mean, α_i is the average effect measure as a deviation from μ, and δ_{ij} is a dominance deviation due to nonadditivity of effects.

In the following developments, the special case of additivity of all gene actions and no epistasis is assumed, hence $\chi_2 - \chi_1 = \chi_1 - \chi_0$, and it can be derived that the genotypic value of the homozygotes AA and aa will always lie symmetrically about the value of the heterozygotes. Then genotypic values expressed in terms of initial gene frequencies can be expressed as in *Form. 21:*

$$X_{AA}^{[n]} = (1-r)^n D^{[0]} C/q_A^{[0]} q_a^{[0]} \text{ and}$$
$$X_{aa}^{[n]} = -(1-r)^n D^{[0]} C/q_A^{[0]} q_a^{[0]},$$
$$\text{where } C = X_2 - X_1.$$

The change in value in the nth generation, as shown in *Form. 22,* is:

$$X_{AA}^{[n]} - X_{AA}^{[n-1]} = -rD^{[n-1]} C/q_A^{[0]} q_a^{[0]}$$
$$X_{aa}^{[n]} - X_{aa}^{[n-1]} = rD^{[n-1]} C/q_A^{[0]} q_a^{[0]}.$$

In the following, the genotypic values are taken as the means of phenotypic distributions of the genotypes and are allowed to change according to the above functions. Initial values of C, D, and the gene frequencies are assumed in order to examine the process for various levels of gene effects and recombination frequencies.

In small population breeding with random mating of selected parents, the probability of attaining any of the possible gene frequencies can be treated as a Markov process with transition probabilities dependent on the relative selective advantage of each genotype, the number of parents and progeny, and the error distribution of individuals around their genotypic means (Hill, 1969). If the relative selective advantages remain constant over generations, then various statistics of allelic fixation rates, effects of dominance, etc., can be studied as functions of the transition matrix (Carr and Nassar, 1970). To study the fixation rates and transition probabilities for a finite number of generations with variable selection effects, the transition matrices for sequential generations must be computed.

For a very large number of loci affecting the quantitative trait, the effect of finite population size on the average disequilibrium effects are expected to be negligible. For any particular "B" locus, the pairwise disequilibrium is substantially affected by finite population sampling and there is a probability distribution for the variations of the associated effect around the expected average effect. However, for many such "B" loci, the average effect is assumed to be more nearly deterministic when taken over all loci for every gamete.

If M monoecious parents are chosen and randomly mated to produce a progeny population of N individuals, from which M parents are subsequently chosen, and if the process is iterated, two stages of sampling are engendered. The gene frequency of the initial M parents defines the sampling populations for the possible gene frequencies of the N progeny. For any mating system, the probabilities of each possible gene and genotypic frequency can be computed. For random mating with a large number of gametes, the probabilities can be computed that N_2 progeny of genotype AA, N_1 of Aa and N_0 of aa are generated assuming a multinomial distribution. The probability of selecting M_2 individuals of AA, M_1 of Aa and M_0 of aa as parents of the succeeding generation is conditional on N_2, N_1 and N_0. This conditional probability is given by Hill (1969) as demonstrated in *Form. 23:*

$$\int_{-\infty}^{+\infty} \prod_{i=i}^{3} \binom{N_i}{M_i} (F_i(x))^{N_i - M_i} (1-F_i(x))^{M_i} \sum_{j=1}^{3} M_j (1-F_j(x))^{-1} f_j(x)dx \quad (1)$$

where: $f_i(x)$ is the density function for genotype i, i = 1, 2, 3, and $F_i(x)$ is the distribution function for genotype i, i = 1, 2, 3.

The product of this conditional probability and the probability of generating the N_i progeny array is the transition probability for change in gene frequency in a single generation. From an initial gene frequency of $2M_2^{|0|} + M_1^{|0|}/2M^{|0|}$, where $M^{|0|}$ is the parental population size, the probability of achieving the next generation's gene frequency, $(2M_2^{|1|} + M_1^{|1|})/2M^{|1|}$, can then be computed.

Tree Breeding Models

For many situations, a normal distribution of individual performances around their genotypic means can be expected. The cumulative distribution function, F_i, and the probability densities, f_i, in (1) can then be taken to be those of normal distribution with appropriate means. The parameters of those functions are assumed to be the mean of the genotype and a common variance (σ^2) around their respective means. The mean effects of the genotypes under an additive, two-allele model in this discussion are determined for several initial conditions of C and initial gene frequencies to simulate populations with different heritability levels for the trait under direct selection. To provide a scale for these effects, C values are determined as if $D^{|0|} = -0.25$, $q_A^{|0|} = 0.5$, $q_B = 0.5$, and $\sigma^2 = 1$, for heritabilites of $h^2 = .010, .026, .50$. For these conditions $C = \sqrt{h^2/.5}$ and h^2 .026, which is in the reported range for growth rates of some tree species (Namkoong *et al.* 1966), corresponds to C = 0.23. In each subsequent generation, the selective differences are dissipated by recombination and the disequilibrium is reduced. Both free recombination (r = 0.50) and tighter linkage (r = 0.25, 0.125, 0.0625) are examined. The difference between homozygotes is reduced by $2rDC/q_A^{|0|}q_a^{|0|}$ in each generation. This value is r times the difference that occurred in the previous generation.

A feasible lower limit to population sizes in tree breeding is four. While most breeding populations are projected to be somewhat larger, subdivisions of even larger populations are not likely to be less than four. Subdivision of the breeding populations as recommended by Baker and Curnow (1969) would require a fairly low upper limit for each

subpopulation. The number of progeny for recurrent selection per population will seldom be smaller than 15 and may often be many times larger. For larger progeny populations, with finite numbers of progeny, parameters for common breeding plans can be estimated. The number of progeny that can be grown is often proportional to the number of parents that can be used in a breeding population. In such cases, the selected population can be nearly fixed, and with some reasonably large progeny populations, the truncation point is approximately fixed. Then the probability of selecting the M_i parents can be computed as multinominal events.

The probabilities are proportional to the relative areas of the genotypic distributions of the M_i genotypes which lie beyond that truncation point. For these investigations, a selection proportion of 10% is arbitrarily chosen. With restricted progeny population sizes, however, the truncation point is a variable and the probabilities are computed by equation (1).

The effects of small population sizes on the probability distribution for gene frequencies can therefore be examined for different parental and progeny population sizes when the selection effects decline as linkage disequilibrium declines. In this paper, parental population sizes M of 4, 8 and 16 are tested with progeny populations N of 16 and 32. In addition, several cases of a large number of progeny with constant selection proportion are examined.

Results

The effects of parental population size on early fixation or loss probabilities are substantial, even without selection (KARLIN and FELDMAN, 1969). With 4-parent breeding, and no selection, the loss of alleles in the first few generations can be high, especially for genes with low (0.125) initial frequencies *(Fig. 1)*. With 8- and 16-parent breeding and no selection, the probabilities of losing alleles of low initial frequencies are still substantial, though perhaps of slightly less concern, and they climb less rapidly. For all population sizes the ultimate probability of loss is the same and equals $1 - q^{|0|}$.

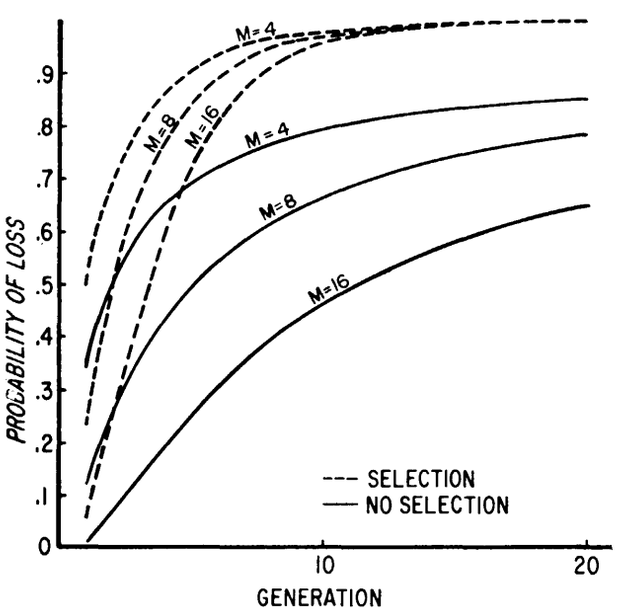

Fig. 1. — Probabilities of loss where M = 4, 8 and 16; h^2 = 0.026; and $q^{|0|}$ = 0.125 for selection without recombination (r = 0) against the allele and for no selection.

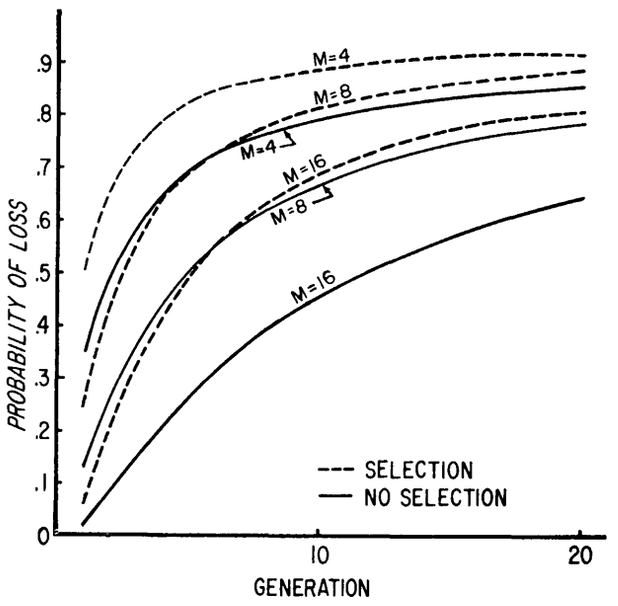

Fig. 2. — Probabilities of loss where M = 4, 8 and 16; h^2 = 0.026; and $q^{|0|}$ = 0.125 for selection with r = 0.5 against the allele and for no selection.

When selection is directly against the allele at locus A, which is of some future value, selection substantially increases the probability of loss at all initial gene frequencies. This effect is demonstrated in *Fig. 1* for a gene frequency of $q^{|0|}$ = 0.125 where A is linked without recombination (r = 0) to loci under direct selection which have a heritability (h^2) of .026.

Under the same conditions but with r = 0.5, the effects of selection are quickly dissipated *(Fig. 2)*. These results indicate that a simple expedient for overcoming the effects of selection on probability of loss of alleles is to double the size of parent population (M). This loss probability with selection is much higher than without selection for the first four generations. After that, transition matrics

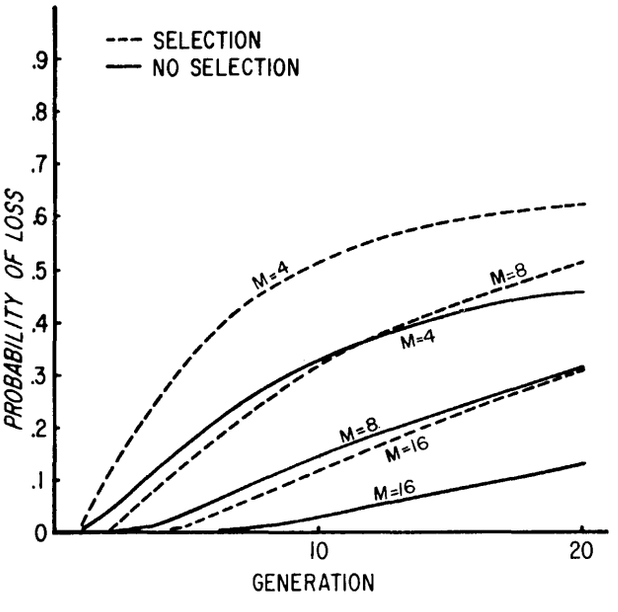

Fig. 3. — Probability of loss where M = 4, 8 and 16; h^2 = 0.026; and $q^{|0|}$ = 0.5 for selection at r = 0.5 against the allele and for no selection.

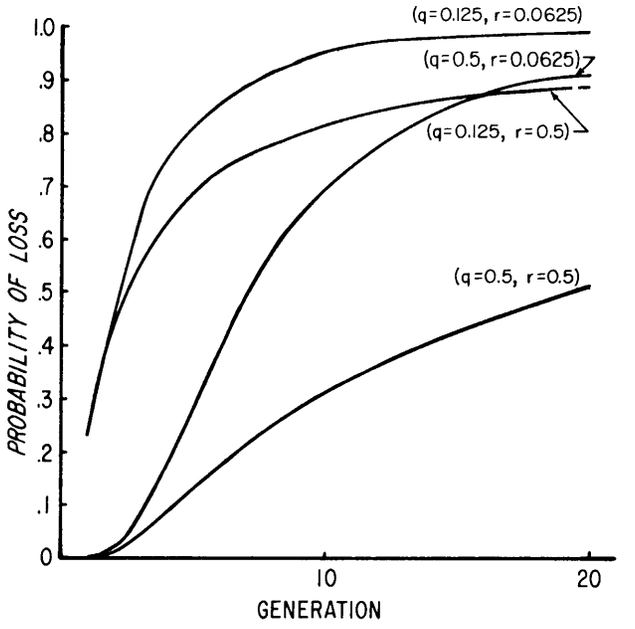

Fig. 4. — Comparisons across recombination rates and gene frequencies for eight parents and infinite numbers of progeny, where $q^{[0]} = 0.5$ or 0.125 and $h^2 = 0.026$.

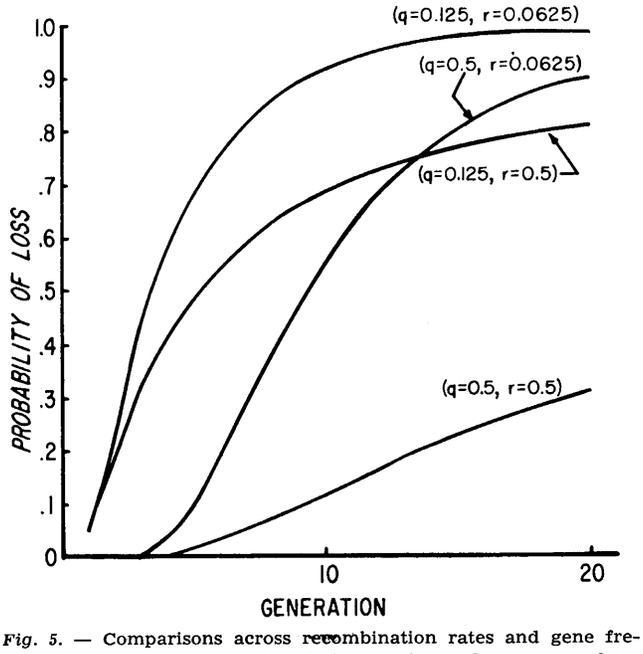

Fig. 5. — Comparisons across recombination rates and gene frequencies for 16 parents and infinite numbers of progeny, where $q^{[0]} = 0.5$ or 0.125 and $h^2 = 0.026$.

with and without selection are similar, and by the eighth generation they are virtually identical. Progress to ultimate fixation is at the same rate for both cases but at a higher level for the case of selection. Doubling the parental population size to avoid increased probability of loss is highly effective in this instance. The effect of selection with M = 8 overcomes the drift effect, and probabilities of loss are slightly greater than with M = 4 and no selection after six generations. Similarly, the loss probabilities for 16-parent breeding with selection are but slightly greater than those for 8-parent breeding without selection after the first six generations. When $q^{[0]}$ is increased to 0.5, the effects of selection are not greatly different than for $q^{[0]} = .125$ *(Fig. 3)*. Again, it appears that loss of neutral genes from early selection can be approximated by doubling the size of the parental population which is undergoing selection of loosely linked loci.

Comparisons of different recombination rates for the same heritabilities, gene frequencies, and population sizes follow expectations. Tighter linkages shift the results from the cases of free recombination towards those of no recombination. Similarly, comparisons of different heritabilities for the same recombination rates, gene frequencies and population sizes merely shift the results from cases of selection with $h^2 = 0.026$ towards that of no selection ($h^2 = 0$), or towards more rapid loss with $h^2 = 0.5$. It is somewhat surprising, however, that tighter linkages can strengthen

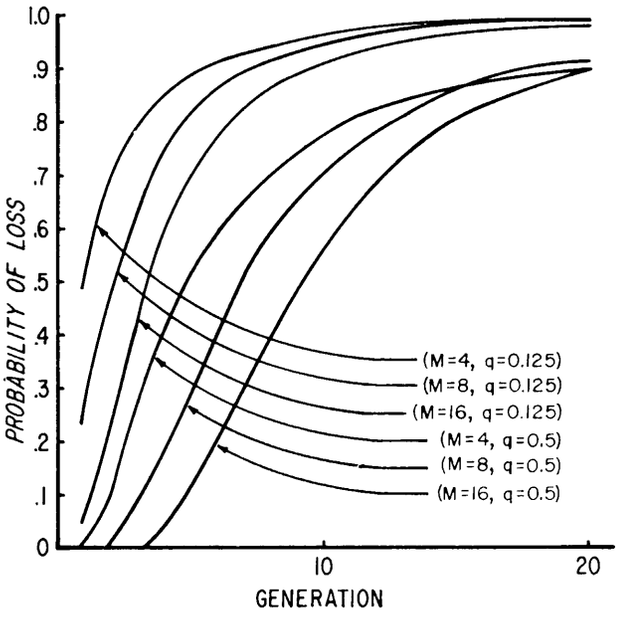

Fig. 6. — Comparison across gene frequencies ($q^{[0]}$) and for numbers of parents (M) where r = 0.0625, $h^2 = 0.026$, and numbers of progeny are infinite.

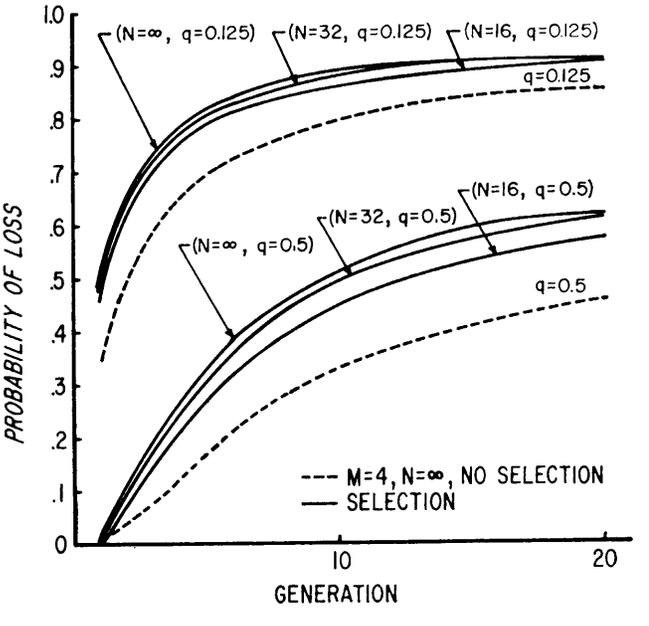

Fig. 7. — Probability of loss for M = 4 under declining selection pressure with restricted progeny populations.

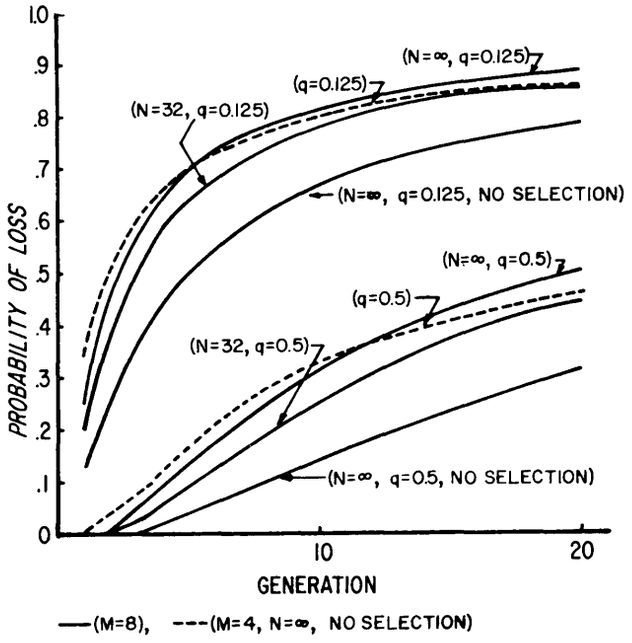

Fig. 8. — Probabilities of loss for M = 8 under declining selection pressure with restricted progeny populations.

the effect of selection and can overcome drift even when initial gene frequencies are low. For example, if M = 8, the probability of loss for $q^{|0|} = 0.125$ and r = 0.5 is eventually lower than for r = 0.0625 *(Fig. 4)*. This effect is more noticeable for M = 16, since the larger population sizes allow the selection effects of the linkage to be more influential *(Fig. 5)*.

The effect of tight linkage in increasing the likelihood of losing the allele of future interest can also be seen with alleles at higher initial gene frequencies, $q^{|0|} = 0.5$ *(Fig. 6)*. Selection effects for the larger population sizes (M = 8) do overcome the inertia of drift for M = 4 and hence more strongly force the loss of the allele of interest.

When the progeny population size is restricted and selection of the next parental generation is consequently limited, the effectiveness of selection is reduced. When this selection is indirect and of rapidly diminishing strength (r = 0.5), the loss of alleles is also slower. In 4-parent breeding, restricting the progeny population to 16 for a selection proportion of 0.25 instead of 0.10 almost halves the differences in loss probabilities between the cases of selection vs. no selection when $q^{|0|} = 0.5$, but the reduction in the effectiveness of selection is less when $q^{|0|} = 0.125$. For 8-parent breeding with a progeny population size of 32, the loss probabilities are similarly affected *(Fig. 8)*.

Breeding Alternatives

When it is necessary to breed in small or subdivided populations, the loss of alleles of a neutral locus (locus A) is rapid and is substantially increased if the alleles are under negative selection pressure. For parental populations of 8 or more, the short-run loss of alleles is a serious problem mainly for low frequency alleles. However, simple expedients such as doubling the parental population size or reducing the progeny population size can diminish the effects of selection. In later generations, however, tight linkage and large parental population size can increase the ultimate probabilities of loss of the alleles of interest.

If subdivided or otherwise small breeding populations are planned, it therefore seems wise to approximately double the size which would give acceptable risks of allelic loss as would be accepted under no selection. For the h^2 and r levels studied, M = 8 gives reasonable probability of loss for early and late selection. Some economies in maintaining these programs may be affected by limiting the progeny population size but at some cost in selection advance.

Literature

BAKER, L. H. and R. N. CURNOW: Choice of population size and use of variation between replicate populations in plant breeding selection. Crop Sci. 9: 555—560 (1969). — CARR, R. N. and R. F. NASSAR: Effects of selection and drift on the dynamics of finite populations. Biometrics 26: 221—228 (1970). — GRIFFING, B.: Theoretical consequences of truncation selection based on the individual phenotype. Aust. J. Biol. Sci. 13: 307—343 (1960) — HILL, W. G.: On the theory of artificial selection in finite populations. Genet. Res. 13: 143—163 (1969). — KARLIN, S. and M. W. FELDMAN: Linkage and selection: new equilibrium properties of the two-locus symmetric viability model. Nat. Acad. Sci. Proc. 62: 70—74 (1969). — KARLIN, S, and J. MCGREGOR: Rates and probabilities of fixation for two locus random mating finite populations without selection. Genetics 58: 141—159 (1968). — NAMKOONG, G., E. B. SNYDER and R. W. STONECYPHER: Heritability and gain concepts for evaluating breeding systems such as seedling seed orchards. Silvae Genet. 16: 76—84 (1966). — SVED, J.: The stability of linked systems of loci with a small population size. Genetics 54: 543—563 (1968).

Changes in the Protein Bands in Pollen grains of Populus ciliata during Storage and its effect on their Viability and Germination

By K. K.DHIR, K. S. CHARK,D. K. KHURANA and I. S. DUA

Department of Botany, Panjab University, Chandigarh-160 014, INDIA

(Received 7th August 1981)

Summary

Disc electrophoresis studies on the pollen grains of *Populus ciliata* revealed the presence of a variety of protein bands depending on the pH of the buffer. Pollen grains on storage at 4° C started losing their viability after three months which also coincided with the simultaneous appearance of new protein bands. It seems that the loss of pollen germinability depends on the appearance of one or, a few inhibitory principles which are probably protein-like.

Key words: *Populus ciliata*, Pollen grains, Proteins, Storage, Germination, Viability.