Selection in Autotetraploids

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Summary. Theoretical studies indicated that response to selection would always be greater in diploid than in autotetraploid populations when gene frequency was the same in both, and that situations in which little or no response to selection could be expected would be more frequent in autotetraploids. Interpretation of the coefficient of selection in terms of escape from infection in a program of selection for disease or insect resistance indicated that moderate levels of escape from infection can drastically reduce response to selection in some cases.

The zygotic constitution of an autotetraploid population will change as it approaches a new random mating equilibrium once selection pressure is relaxed. The changes will result in no change in the population mean if the trait under selection exhibits no dominance, but the mean will decrease slightly if there is dominance.

Introduction

Relatively simple selection procedures have been effective in improvement of several characters in alfalfa, *Medicago sativa* L., (Hill, et al., 1969 and Elgin, et al., 1970). Although most genetic evidence indicates that alfalfa is autotetraploid (Stanford and Clement, 1958), a thorough examination of the behavior of simple autotetraploid populations under selection from a plant breeding viewpoint is lacking. Selection in autotetraploid populations was examined by Haldane (1926) and Wright (1938), but they were concerned mostly with relatively mild natural selection and did not consider various genetic models in detail. Plant breeders usually practice more stringent selection in order to obtain greater gain in selection experiments. A comparison of different genetic models under selection in autotetraploids and the effects of different coefficients of selection with these models is the subject of this paper.

Algebra of Two-Allele Autotetraploid Populations

The frequencies and gametes produced by each of the genotypes in a two-allele autotetraploid population are given in Table 1, where x_n, $2 y_n$, and z_n are the frequencies of gametes AA, Aa, and aa, respectively. Random chromosome segregation (no double reduction) was assumed in all phases of this study. The subscript, n, indicates the generation and is coded so that gametes belong to the same generation as the zygotes they form. If the population is in random mating equilibrium, $x_n = p^2$, $y_n = p q$, and $z_n = q^2$, where $p =$ the frequency of allele A and $q = = 1 - p =$ the frequency of allele a. Kempthorne (1957) showed that an autotetraploid population approaches random mating equilibrium asymptotically once it has been removed from it. Even when the population is not in random mating equilibrium,

the following equalities hold:

$$x_n + y_n = p_n$$
$$y_n + z_n = q_n$$
$$x_n + 2 y_n + z_n = 1 \ .$$

The population is completely specified by z_n and q_n, because all other parameters can be calculated when these two are known.

Gamete frequencies in generation $n + 1$ are calculated as follows:

$$x_{n+1} = \left(w_{1j} x_n^2 + 2 w_{2j} x_n y_n + (w_{3j}/3) \times \right.$$
$$\left. \times (x_n z_n + 2 y_n^2) \right)/ \ \bar{w}_{.j}$$

$$y_{n+1} = \left(w_2 x_n y_n + (2 w_{3j}/3) (x_n z_n + 2 y_n^2) + \right.$$
$$\left. + w_{4j} y_n z_n \right)/\bar{w}_{.j}$$

$$z_{n+1} = \left((w_{3j}/3) (x_n z_n + 2 y_n^2) + 2 w_{4j} y_n z_n + \right.$$
$$\left. + w_{5j} z_n^2 \right)/\bar{w}_{.j}$$

where $w_{ij} =$ the value of the ith genotype in the jth genetic model and $\bar{w}_{.j} = \sum_i f_i w_{ij}$ (where $f_i =$ the frequency of the ith genotype). Division by $\bar{w}_{.j}$ is necessary to make $x_{n+1} + 2 y_{n+1} + z_{n+1} = 1$. All w_{ij} and $\bar{w}_{.j} = 1$ in the absence of selection. The zygotic frequencies in generation $n + 1$ are obtained by expansion of $(x_{n+1} + 2 y_{n+1} + z_{n+1})^2$.

Selection in Autotetraploids with Different Conditions of Dominance

When selection is practiced in a population, some of the genotypes contribute less to the succeeding population than others. This can be expressed by the coefficient of selection, s, which is defined here almost exactly as it was defined for diploids by Falconer (1960). The contribution of the favored genotype is defined to be 1 and that of the genotype selected against to be $1 - s$. In plant breeding problems, s is

a measure of the ability to avoid undesirable genotypes in the sample selected in each generation. No undesirable individuals will be included in the selected group when $s = 1$.

A large number of possible conditions of dominance exist in autotetraploids. Five were investigated in this study: no dominance with selection against allele a (Model I); complete dominance with selection against the recessive homozygote (Model II); complete dominance with selection against those individuals with one or more dominant alleles (Model III); duplex dominance with selection against -aaa genotypes (Model IV); and overdominance (Model V). Solutions when selection is against allele A, against genotype $AAAA$, against genotype ---a, or against genotype AAA- can be obtained by interchanging p and q in models I, II, III, and IV, respectively. Thus, these specific examples are not presented. Any specific example can be calculated by using the procedures given above.

Model I. The desirability of the genotypes with this model is in direct proportion to the number of A alleles (Table 1). After algebraic simplification, the parameters for this model are:

$$\bar{w}._1 = 1 - s\, q_n$$

$$z_{n+1} = [(z_n/3)\,(1 - s/2) + (2\,s\,q_n^2/3)\,(1 - s/2) - (s\,z_n\,q_n/2)]/\bar{w}._1$$

$$q_{n+1} = [q_n - (s/4)\,(q_n + z_n + 2\,q_n^2)]/\bar{w}._1$$

$$\Delta q = q_{n+1} - q_n = \frac{-\,s\,(p_n\,q_n - (z_n - q_n^2))}{4\,(1 - s\,q_n)}.$$

Δq is negative since selection pressure eliminates some of the genotypes which contain recessive alleles. If the initial population is in random mating equilibrium, $z_0 = q_0^2$, and $\Delta q = s\,p\,q/4\,(1 - s\,q)$ for the first cycle of selection. Falconer (1960) showed that $\Delta q = s\,p\,q/2\,(1 - s\,q)$ for diploids. When q is the same for both levels of ploidy, response to selection (Δq) is one-half as great in autotetraploids as in diploids since $\Delta q_{4\,k}/\Delta q_{2\,k} = 1/2$. This relationship does not hold for continued selection because one cycle of selection in autotetraploids will destroy the random mating equilibrium.

Model II. The recessive homozygote is undesirable and the remaining genotypes are indistinguishable

with this model. The parameters for Model II are:

$$\bar{w}._{II} = 1 - s\,z_n^2$$

$$z_{n+1} = ((z_n/3) + (2\,q_n^2/3) - s\,z_n^2)/\bar{w}._{II}$$

$$q_{n+1} = (q_n - s\,z_n^2)/\bar{w}._{II}$$

$$\Delta q = q_{n+1} - q_n = -\,s\,z_n^2\,p_n/\bar{w}._{II}.$$

Δq is negative with this model also, because selection is against the recessive homozygote which reduces the value of q. It is possible that no response to selection would be observed when potential variability is present in the population, because it is possible that $z_n = 0$ when $q_n \neq 0$. If the initial population consisted of progenies from only $AAAA$ and $AAAa$ genotypes, $z_1 = 0$ when $q_1 \neq 0$. $aaaa$ genotypes would not occur in the first generation, but would appear as the population approached random mating equilibrium. Autotetraploid populations have much greater capacity to mask recessive alleles than diploid populations.

When the initial cycle of selection is in a random mating equilibrium population, $\Delta q_{4\,k} = -\,s\,p\,q^4/(1 - s\,q^4)$, which has a form similar to that for diploids; $\Delta q_{2\,k} = -\,s\,p\,q^2/(1 - s\,q^2)$ (Falconer, 1960). Response is always greater in diploid than in autotetraploid populations with the same value of q, because $\Delta q_{4\,k}/\Delta q_{2\,k} = (q^2 - s\,q^4)/(1 - s\,q^4) < 1$ for all values of q between 0 and 1.

Model III. The recessive homozygote is the most desirable genotype and all genotypes with a dominant allele are considered equally undesirable with this model. The parameters for this model are:

$$\bar{w}._{III} = 1 - s\,(1 - z_n^2)$$

$$z_{n+1} = ((z_n/3)\,(1 - s) + (2\,q_n^2/3)\,(1 - s) + s\,z_n^2)/\bar{w}._{III}$$

$$q_{n+1} = (q_n\,(1 - s) + s\,z_n^2)/\bar{w}._{III}$$

$$\Delta q = q_{n+1} - q_n = s\,z_n^2\,p_n/\bar{w}._{III}.$$

Δq is positive with Model III because selection is for the recessive homozygote which tends to increase the value of q. As with Model II, the possibility of no response to selection when heterozygosity is present in the population exists in Model III.

Δq for one cycle of selection in an autotetraploid population which is in random mating equilibrium is $s\,pq^4/(1 - s\,(1 - q^4))$, and it is $s\,pq^2/(1 - s\,(1 - q^2))$ for diploids (Falconer, 1960). When q is the same for both levels of ploidy, response is greater in diploid

Table 1. *Frequencies, gametic products, and values under different genetic models for the genotypes in a two-allele autotetraploid population*

Genotype	Frequency	Gametic products			Values for different genetic models				
		AA	Aa	aa	I	II	III	IV	V
$AAAA$	x_n^2	1			1	1	$1 - s$	1	$1 - s_1$
$AAAa$	$4\,x_n\,y_n$	1/2	1/2		$1 - s/4$	1	$1 - s$	1	$1 - s_2$
$AAaa$	$2\,x_n\,z_n + 4\,y_n^2$	1/6	4/6	1/6	$1 - s/2$	1	$1 - s$	1	1
$Aaaa$	$4\,y_n\,z_n$		1/2	1/2	$1 - 3\,s/4$	1	$1 - s$	$1 - s$	$1 - s_3$
$aaaa$	z_n^2			1	$1 - s$	$1 - s$	1	$1 - s$	$1 - s_4$

than in autotetraploid populations. This can be demonstrated as follows:

$$\Delta q_{4\,h}/\Delta q_{2\,h} = q^2 \left(1 - s \left(1 - q^2\right)\right)/\left(1 - s \left(1 - q^4\right)\right) < 1$$

for all values of q between 0 and 1.

Model IV. Duplex dominance has been demonstrated in alfalfa (Stanford, 1959). The *aaaa* and *Aaaa* genotypes are selected against and the *AAaa*, *AAAa*, and *AAAA* genotypes are equally favorable with this model (Table 1). Another variation of this model which theoretically exists is that *Aaaa* and *aaaa* genotypes have different selection coefficients. This variation is not presented here, but the necessary calculations are a simple extension of those presented. The parameters for this model are:

$$\bar{w}._{IV} = -1 - s \left(4 \, y_n \, z_n + z_n^2\right)$$

$$z_{n+1} = \left((z_n/3) + (2 \, q_n^2/3) - 2 \, s \, z_n \, q_n - s \, z_n^2\right)/\bar{w}._{IV}$$

$$q_{n+1} = \left(q_n - 3 \, s \, z_n \, q_n + 2 \, s \, z_n^2\right)/\bar{w}._{IV}$$

$$\Delta q = q_{n+1} - q_n = \left(-3 \, s \, z_n \, p_n^2 \, q_n + s \, z_n \, (z_n - q_n^2) \times \right.$$
$$\left. (2 \, p - q)\right)/\bar{w}._{IV} .$$

When the initial cycle of selection is in a population which is in random mating equilibrium, $\Delta q = -3 \, s \, p^2 \, q^2/(1 - s \, q^3 \, (4 \, p + q))$. No counterpart to the duplex dominance model exists in diploids.

Model V. Many types of overdominance are theoretically possible in autotetraploids because there are three different heterozygous genotypes with only two alleles. The duplex (*AAaa*) was assumed to be the most favored genotype with each of the remaining genotypes having their own selection coefficient (Table 1). The parameters for this model are:

$$\bar{w}._{V} = 1 - s_1 \, x_n^2 - 4 \, s_2 \, x_n \, y_n - 4 \, s_3 \, y_n \, z_n - s_4 \, z_n^2$$

$$z_{n+1} = \left((z_n/3) + (2 \, q_n^2/3) - 2 \, s_3 \, y_n \, z_n - s_4 \, z_n^2\right)/\bar{w}._{V}$$

$$q_{n+1} = \left(q_n - s_2 \, x_n \, y_n - 3 \, s_3 \, y_n \, z_n - s_4 \, z_n^2\right)/\bar{w}._{V}$$

$$\Delta q = q_{n+1} - q_n = \left(s_1 \, x_n^2 \, q_n - s_4 \, z_n^2 \, p_n + \right.$$
$$\left. + y \, (s_2 \, x \, (3 \, q - p) - s_3 \, z \, (3 \, p - q))\right)/\bar{w}._{V} .$$

If the initial cycle of selection is in a population which is in random mating equilibrium:

$$\Delta q = p \, q \, \left((s_1 \, p^3 - s_4 \, q^3) + (s_2 \, p^2 \, (3 \, q - p) - \right.$$
$$\left. s_3 \, q^2 \, (3 \, p - q))\right)/\bar{w}._{V} .$$

Falconer (1960) showed that for diploids:

$$\Delta q = p \, q \, (s_1 \, p - s_2 \, q)/(1 - s_1 \, p^2 - s_2 \, q^2) .$$

It can be seen that overdominance can be more complicated in autotetraploids than in diploids. Unlike models I through IV in autotetraploids, a stable equilibrium (numerator of $\Delta q = 0$) can exist for values of q other than 0 or 1. A general solution for the equilibrium values could not be found, but several examples were examined for an initial cycle of selection in a population which is in random mating equilibrium.

1) $s_2 = s_3 = 0$, all heterozygotes have equal value and are greater than either homozygote. In this

sample, the numerator of Δq reduces to $p \, q \, (s_1 \, p^3 - s_4 \, q^3)$, and equilibrium values are:

$$q = 0, 1, \text{ and } 1/(1 + (s_4/s_1)^{1/3}) .$$

2) $s_2 = (1/4) \, s_1$, $s_3 = (1/4) \, s_4$, the duplex is the most desirable genotype and the triplex (*AAAa*) and simplex (*Aaaa*) have values between the duplex and their most similar homozygote (*AAAA* and *aaaa*, respectively). The numerator in this example reduces to $(3/4) \, p \, q \, (s_1 \, p^2 - s_4 \, p^2)$, and equilibrium values are

$$q = 0, 1, \text{ and } 1/(1 + (s_4/s_1)^{1/2}) .$$

3) $s_1 = s_2$, $s_3 = s_4$, the duplex is the most favored genotype, and the remaining heterozygotes have value equal to their most similar homozygotes. The numerator in this example is $3 \, p^2 \, q^2 \, (s_1 \, p - s_4 \, q)$, and equilibrium values are:

$$q = 0, 1, \text{ and } 1/(1 + (s_4/s_1)) .$$

Equilibrium values with this example are the same as with diploids (Falconer, 1960). An equilibrium exists when $q = 1/2$ in each of the above examples when the homozygotes have equal value.

There are actually five equilibrium values of q with overdominance in autotetraploids, since the equation for Δq is a fifth degree polynomial and equilibrium values correspond to roots of the polynomial. However, the remaining two roots in all examples examined were for values of q which are impossible genetically (imaginary or outside the range of 0 to 1).

Comparison of models. Response to selection, Δq, in each of the models depends on the selection coefficient, s and the state of the population at the time selection is practiced, because Δq is a function of s and the parameters which define the population. If the initial cycle of selection is in a population which is in random mating equilibrium, response is completely determined by the values of s and q at the time selection is practiced. Response for later cycles of selection, or response in a population not in random mating equilibrium is more complicated because the disequilibrium of the population must be taken into consideration when calculating response.

Δq for an initial cycle of selection in a population in random mating equilibrium with various values of q was compared for each of the models (Figure 1). The response curves for diploid populations were included where appropriate. Δq is negative in Models I, II, and III (Figure 1-A, -B, and -D, respectively) and successful selection will decrease the value of q; Δq is positive in Model III (Figure 1-C) and successful selection will increase the value of q.

The graphs illustrate the fact that response is greater in diploid than in autotetraploid populations for all models which can be compared when q is the same for both levels of ploidy. Selection for traits which exhibit no dominance (Model I, Figure 1-A), traits which are determined by a completely dominant allele (Model II, Figure 1-B), and traits which have

a duplex dominance inheritance pattern (Model IV, Figure 1-D) should be successful in unimproved populations. The goal of selection with each of these models is to decrease the value of q. Thus, selection would be practiced in populations with large values of q, and response is greater when q is large for each of these models. Response decreases rapidly as q decreases in Models II and IV with autotetraploids. However, this is not very serious unless the recessive allele must
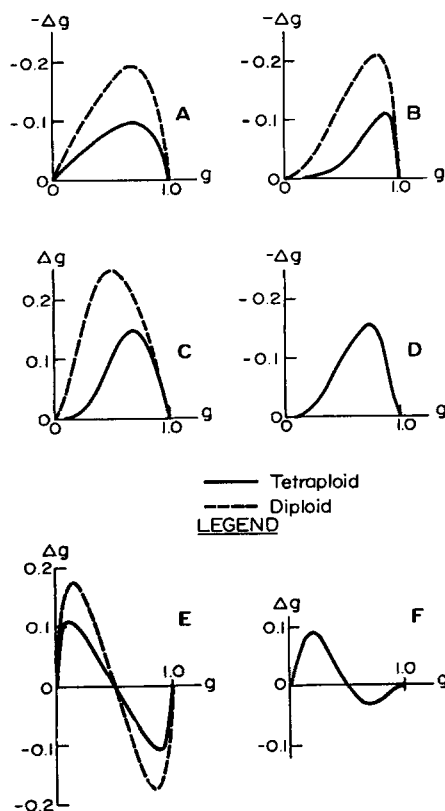

Fig. 1. Change in gene frequency, Δq, with value of q for different genetic models. A $=$ no dominance with selection against allele a, B $=$ complete dominance with selection against $aaaa$ genotypes, C $=$ complete dominance with selection against A--- genotypes, D $=$ duplex dominance with selection against $-aaa$ genotypes, E $=$ overdominance with selection against $AAAA$ and $aaaa$ genotypes, and F $=$ overdominance with selection against all but the duplex, $AAaa$ genotype. $s = 0.8$ for all models

be competely eliminated from the population. The frequency of undesirable genotypes with q less than 0.5 with Model II or 0.25 with Model IV can easily be tolerated for most characters in crops such as alfalfa.

It is possible that little or no response would result from selection in some unimproved populations when the desirable genotype is the recessive homozygote (Model III, Figure 1-C) and s is less than 1.0. The frequency of the desirable genotype would be low when q is small, and Δq is very small when q is small, and s is less than 1.0. Of course, the desired goal can be reached in one cycle of selection when $s = 1.0$.

Effects of the Selection Coefficient

The coefficient of selection, s is vital to selection progress. All of the equations for response indicate that greater response will be achieved with larger values of s. In programs of selection for disease or insect resistance, $1 - s$ is the probability that the susceptible genotypes will appear resistant or escape infection. The constitution of the selected group would be $(1 - s)$ (frequency of undesirable genotypes) $+$ (frequency of desirable genotypes). Therefore, effects of smaller values of s are more serious when the frequency of the desirable genotype is low.

Apparently, algebraic expressions for the gamete frequencies of generation n in terms of their frequencies in generation 0 for selection in autotetraploids do not exist in a form simple enough for analytic comparisons. Approximations require such drastic assumptions that their value is questionable. However, expected frequencies for successive generations of selection for different values of s can easily be computed on a desk-top computer. Procedures for doing this are given in the above section on algebra of autotetraploid populations. Genotypic values indicative of the coefficients of selection for the genotypes were assumed for autotetraploid models I, II, III, and IV (Table 2), and the expected means of the population for 15 successive generations of selection were computed for $s = 0.7$, 0.8, 0.9, 0.95, and 1.0 (Figure 2). The means are the total frequency of desirable genotypes (weighted according to value in Model I) in the population. Initial values of q were chosen so that initial frequencies of desirable individuals were low and approximately equal with each model. The initial population was assumed to be in random mating equilibrium.

As expected, smaller values of s always resulted in slower response to selection (Figure 2). Varying the value of s had the greatest effect with no dominance (Model I), and with complete dominance when selection was against the recessive homozygote (Model III). Less than half the response was obtained with $s = 0.7$ as compared to s greater than 0.9 with 15 generations of selection in Model I, and practically no response to selection was observed in 15 generations of selection with $s = 0.7$ in Model III. Very little response occurred in the first three or four generations of selection with Model I or III when s was less than 1.0. A plant

Table 2. *Initial values of q and genotypic values assumed in the examples of successive generations of selection with indicated genetic models in autotetraploids*

Initial	Genotypes				
Model q	$AAAA$	$AAAa$	$AAaa$	$Aaaa$	$aaaa$
I .999	1	3/4	1/2	1/4	0
II .999	1	1	1	1	0
III .200	0	0	0	0	1
IV .95	1	1	1	0	0

breeder could conclude that he was working with a complex-inherited trait in either case when the problem was actually a small or intermediate value of s.

Varying the value of s did not have as great an effect on response to selection with dominance and selection against the recessive homozygote (Model II) or with duplex dominance (Model IV). Although smaller values of s resulted in a reduced response to selection, response was observed in the early generations, and good response was obtained by five or six generations of selection for most values of s.

A low frequency of desirable genotypes was assumed in the initial generation of selection with each of the models presented in Figure 2. The rate of response increases as selection proceeds in such populations because selection is changing gene frequency to values more favorable to selection response. This indicates that persistence in selection programs will often pay off, especially when the desirable genotypes are at very low frequencies at the time selection is initiated. A greater response was observed in the last three generations of selection for resistance to yellowing caused by the potato leafhopper (*Empoasca fabae*, Harris) in alfalfa than in the first eight cycles (Hill, et al., 1969).

Plant breeders should strive to make the selection coefficient, s, as large as possible in order to obtain maximum response to selection. $1 - s$ can be equated with the probability of escape from infection in programs of selection for disease and insect resistance. Efforts to reduce escape from infection (increase the value of s) will increase response to selection, especially in populations in which the frequency of desirable genotypes is low. As many as 64% of the alfalfa plants tested escaped infection by *Uromyces striatus* Schroet. var. *medicaginis* (Pass.) Arth. (alfalfa rust) in one study conducted in the field (Hill et al., 1963). Only 58 of approximately 3500 (1.7%) of the susceptible plants escaped infection by *Pseudopeziza medicaginis* (Lib.) Sacc. (alfalfa common leafspot) in another study conducted in the greenhouse and growth chamber (unpublished results, U.S. Regional Pasture Research Laboratory). Although these studies were with different pathogens, they support the general claim that better control of escape from infection is obtained with artificial inoculation techniques. Selection based on natural epiphytotics will often be ineffective, and the breeder must use artificial inoculation techniques if he is to expect continued success in a selection program.

Population Changes when Selection is Relaxed

Shifts will occur in autotetraploid populations once selection is relaxed because the population will approach a new random mating equilibrium in the absence of selection. If x_n, $2 y_n$, and z_n are frequencies of AA, Aa, and aa gametes, respectively, from the group of plants selected in the last generation of
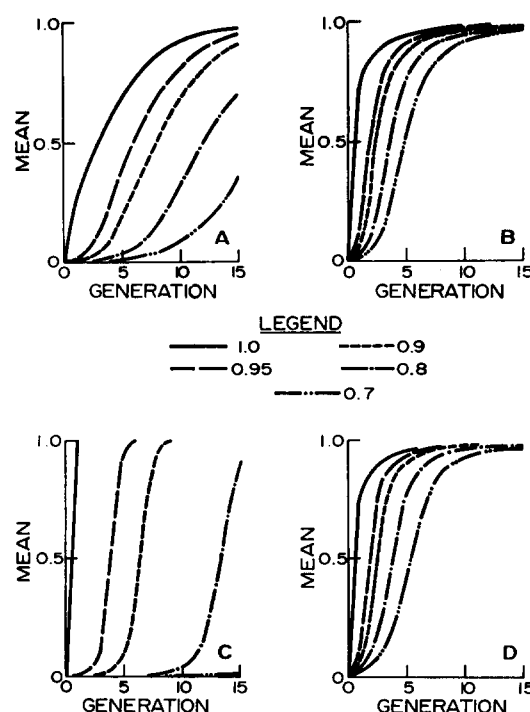

Fig. 2. Change in population mean with successive generations of selection in indicated autotetraploid population. Values of s are given in the legend

selection, the means of the population resulting from random mating of the selected plants will be p, $1 - z_n^2$, and z_n^2 for Models I, II, and III, respectively. Kempthorne (1957) has shown that:

$$x_{n+k} = p_n^2 + (1/3)^k d$$

$$y_{n+k} = p_n q_n - (1/3)^k d$$

$$z_{n+k} = q_n^2 + (1/3)^k d$$

where k indicates the kth generation of random mating without selection and $d = x_n z_n - y_n^2$ is a measure of the random mating disequilibrium. Thus, the population means will approach p_n, $1 - q_n^4$, and q_n^4 for Models I, II, and III, respectively, as the population approaches random mating equilibrium.

The mean will not change with approach to random mating equilibrium in Model I, although changes will occur in the genotypic constitution of the population as it approaches equilibrium. The shifts $(\mu_n - \mu_{RME})$ for Models II and III will be $- (z_n^2 - q_n^4)$ and $(z_n^2 - q_n^4)$, respectively, where $\mu_n =$ the mean at the time selection is relaxed and $\mu_{RME} =$ the mean at equilibrium. The quantity $(z_n^2) - (q_n^4)$ can be written as $(z_n - q_n^2) \times (z_n + q_n^2)$. $(z_n + q_n^2)$ is always positive and the direction of the shift with approach to random mating equilibrium can be determined by determining the sign of $(z_n - q_n^2)$.

For Model II:

$$z_{n+1} - q_{n+1}^2 = ((1/3) (z_n - q_n^2) (1 - s z_n^2) - s z_n^2 p_n^2)/\bar{w}_{II_n}$$

If the initial population was in random mating equilibrium:

$$z_1 - q_2^1 = - s\, q_0^2\, p_0^4/\overline{w}_{II}\ .$$

Starting with $(z_1 - q_1^2)$ and using the general form to compute the difference to generation n, only negative terms enter into the numerator. Therefore, $z_n - q_n^2 < 0$ for all generations of selection and $\mu_n - \mu_{RME} > 0$, indicating that the mean will decrease as the population approaches random mating equilibrium once selection is relaxed.

For Model III:

$$z_{n+1} - q_{n+1}^2 = ((1/3)\,(1-s)\,(z_n - q_n^2) \times$$
$$(1 - s + s\, z_n^2) + s\,(1-s)\, z_n^2\, p_n^2)/\overline{w}_{III_n}$$

and $z_1 - q_1^2 = s\,(1-s)\, q_0^4\, p_0^2/\overline{w}_{III}$ if the population was in random mating equilibrium when selection began. Arguments similar to those used in Model II above show that $z_n - q_n^2 > 0$ for all generation of selection. Thus, $\mu_n - \mu_{RME} > 0$, indicating that the mean will decrease as the population approaches equilibrium once selection is relaxed with Model III also.

It can be shown that $|z_n^2 - q_n^4| < \mu_n\,(1 - \mu_n)$: For Model II, $\mu_n = 1 - z_n^2$, which implies that $z_n = (1 - \mu_n)^{1/2}$. $y_n + z_n = q_n$ for all generations, which implies that $q_n > (1 - \mu_n)^{1/2}$, which further implies that $q_n^4 > (1 - \mu_n)^2$. $\mu_n = z_n^2$ for Model III, and a similar argument shows that $q_n^4 > \mu_n^2$. Substitution of the upper limit of q_n^4 into $|z_n^2 - q_n^4|$ gives the desired results. Therefore, the change in the population mean with approach to random mating equilibrium will be less than $\mu_n\, x\,(1 - \mu_n)$ with either model. The change in the mean will not be very large if proportion of desirable genotypes (population mean) is large at the time selection is relaxed.

Attempts to express the change in the population mean with approach to random mating equilibrium for Model IV in a form similar to those for Models II and III were unsuccessful. However, studies of the change on a computer indicated that the change would be small in most cases, but could be in either direction, depending on the state of the population at the time selection was relaxed.

Selection will not likely fix gene frequency with either genetic model. Therefore, the potential for selection in the opposite direction will almost always exist in the populations which have been improved by selection. Plant breeders must take some measures to insure that natural selection, correlated response to selection for other traits, and chance variations will not destroy improvements previously developed in the populations with which they are working.

Literature

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