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Comparison of Selection Methods for Autotetraploids. I. Theoretical[1]

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ABSTRACT

The relative effectiveness of selfed progeny test, selfed family, polycross progeny test, polycross family, full-sib family, and individual selection was compared theoretically. Initial gene frequency, level of environmental variance, and level of dominance were variables in the comparisons. The comparisons were based on theoretical changes in gene frequencies with one cycle of selection in two-allele autotetraploid populations that were in random-mating equilibrium.

Theoretical responses with selfed progeny test and selfed family selection were equal and always greater than the other methods. Polycross progeny test selection was the second most effective method, and polycross family selection was the least effective method. Full-sib family and individual selection were intermediate between polycross progeny test and polycross family selection. Full-sib family selection was more effective than individual selection when environmental variance was large, but individual selection was more effective for some gene frequencies when environmental variance was small.

Additional index words: Family selection, Mass selection, Progeny test.

PLANT breeders faced with ineffectiveness in a selection program have two alternatives: refining techniques to make selection more accurate or using different methods of selection. Theoretical studies of different methods of selection for diploid species are abundant (Falconer, 1960; Sprague, 1966), but theory is much less developed for autotetraploid species. A theoretical comparison of six methods of selection that may be used in autotetraploids such as alfalfa (*Medicago sativa* L.) is presented herein.

MATERIALS AND METHODS

The methods of selection we evaluated may be divided into three classes: (1) Individual selection, in which the best individuals in the population are selected on the basis of their phenotypic performance and intermated to form the improved population. This method has also been called recurrent phenotypic selection (Dudley, Hill, and Hanson, 1963) and simple recurrent selection (Allard, 1960) in plant breeding literature. (2) Progeny test selection, in which plants are selected on the basis of the mean performance of their progenies. We examined polycross and selfed progeny test selection. (3) Family selection, in which all individuals within the best families are selected and intermated to produce the improved population. Polycross, full-sib, and selfed family selection were examined. We did not evaluate within-family or combined family-within-family selection (Falconer, 1960).

The methods of selection were evaluated by assuming that change in gene frequency was proportional to $\mathrm{Cov}(x,y)/\sigma_y$, where $\mathrm{Cov}(x,y)$ is the covariance between gene frequency in the individuals to be considered for selection and the mean of the individuals upon which the selection is based, and σ_y is the phenotypic standard error of the individuals upon which selection is based. The initial population was assumed to be

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Table 1. Genotypes, frequencies, mean gene frequencies, and means for indicated family types in a two-allele autotetraploid population.*

Genotype i		Family type: Individual x_{I_i}	Individual y_{I_i}	Polycross x_{P_i}	Polycross y_{P_i}	Selfed x_{S_i}	Selfed y_{S_i}
AAAA	p^4	0	$4A + 6D + 4T + F$	$\frac{q}{2}$	$(4p+2q)A + (6p^2+6pq+q^2)D + (4p^2+2pq)T + p^2F$	0	$4A + 6D + 4T + F$
AAAa	$4p^3q$	$\frac{1}{4}$	$3A + 3D + T$	$\frac{(p+5q)}{8}$	$\frac{(7p+3q)A}{2} + \frac{(9p^2+8pq+p^2)D}{2} + \frac{(5p^2+2pq)T}{2} + \frac{p^2F}{2}$	$\frac{1}{4}$	$3A + \frac{13D}{4} + \frac{6T}{4} + \frac{F}{4}$
AAaa	$6p^2q^2$	$\frac{1}{2}$	$2A + D$	$\frac{(p+3q)}{4}$	$(3p+q)A + \frac{(19p^2+14pq+q^2)D}{6} + \frac{(4p^2+pq)T}{3} + \frac{p^2F}{6}$	$\frac{1}{2}$	$2A + \frac{8D}{6} + \frac{2T}{6} + \frac{F}{36}$
Aaaa	$4pq^3$	$\frac{3}{4}$	A	$\frac{(3p+7q)}{8}$	$\frac{(5p+q)A}{2} + (2p^2+pq)D + \frac{p^2T}{2}$	$\frac{3}{4}$	$A + \frac{D}{4}$
aaaa	q^4	1	0	$\frac{(p+2q)}{2}$	$2pA + p^2D$	1	0

* x_{I_i}, x_{P_i}, and x_{S_i} represent mean gene frequencies within individuals, polycross families, and selfed families, respectively. y_{I_i}, y_{P_i}, and y_{S_i} represent mean genotypic values for individuals, polycross families, and selfed families, respectively.

a two-allele autotetraploid population in random mating equilibrium. Values of (4A + 6D + 4T + F), (3A + 3D +T), (2A + D), (A), and (O), respectively, were assigned to the *AAAA*, *AAAa*, *AAaa*, *Aaaa*, and *aaaa genotypes* (Table 1). Genetic interpretation of the parameters in this model were given by Hill (1971b). The covariances [Cov (x,y)] for different methods of selection were derived from the parameters in Table 1 as follows:

Individual: $\Sigma f_i x_{I_i} y_{I_i} - (\Sigma f_i x_{I_i})(\Sigma f_i y_{I_i})$

Polycross progeny test: $\Sigma f_i x_{I_i} y_{P_i} - (\Sigma f_i x_{I_i})(\Sigma f_i y_{P_i})$

Polycross family: $\Sigma f_i x_{P_i} y_{P_i} - (\Sigma f_i x_{P_i})(\Sigma f_i y_{P_i})$

Selfed progeny test: $\Sigma f_i x_{I_i} y_{S_i} - (\Sigma f_i x_{I_i})(\Sigma f_i y_{S_i})$

The covariance for selfed family selection was the same as that for selfed progeny test selection, because gene frequency within selfed families is the same as in the parents ($x_{I_i} = x_{S_i}$). The phenotypic variance, σ^2_y, was assumed to be $\sigma^2_E + \sigma^2_G$ for individual selection and $(\sigma^2_E + \sigma^2_G - \sigma^2_F)/n + \sigma^2_F$ for progeny test and family selection, where σ^2_E, σ^2_G, σ^2_F, and n represent environmental variance, total genetic variance, the variance among family means, and the number of individuals per family, respectively.

The covariance between the average gene frequency in the 15 possible full-sib families of the population and their means was computed in a manner similar to that above. The details are not presented here.

Use of the above approach for theoretical evaluation of breeding methods was advocated by Robertson (1963). The relationship between this and other methods of evaluating changes in gene frequency is described for diploids by Falconer (1960). The same general approach was used by Comstock, Robinson, and Harvey (1949) to compare different methods of recurrent selection used in the breeding of *Zea mays* L.

Numerical comparisons of the methods of selection were obtained by computation of the values of $\mathrm{Cov}(x,y)/\sigma_y$ for different gene frequencies with each of the methods of selection. Information on the effects of different genetic models was obtained by changing the values of A, D, T, and F (Table 1). The effects of different magnitudes of environmental variance and family size were assessed by inserting different values for σ^2_E and n into the equation for σ^2_y. Values of 0.0675 and 0.4275 were used to represent low and high values of σ^2_E in all comparisons presented herein. These values of σ^2_E represent theoretical heritabilities of 25 and 5%, respectively, when p = 0.1, A = 0.25, and D = T = F = 0 in our assumed population (Table 1). All comparisons presented in this paper are for n = 10.

RESULTS

The covariances, or numerators, of each of the methods of selection except selfed family and selfed progeny test were a constant times pqα (Table 2). The covariances are negative because of the coding used in Table 1 and the fact that selection is against the recessive allele. The numerator for individual selection was twice as large as the numerators for polycross progeny test or full-sib family selection. The numerator was the smallest for polycross family selection. The numerators for selfed family and selfed progeny test selection were similar to the one for individual selection, but were identical to it only when there was no nonadditive gene action (D = T =F = 0). The covariance for selfed family and selfed progeny test selection could not be written in terms of α, as was done with the other methods.

Table 2. Equations for change in gene frequency with indicated method of selection.

Method	Equation*
Individual	$\frac{-pq\,\alpha}{[\sigma^2_E + \sigma^2_G]^{1/2}}$
Polycross progeny test	$\frac{-pq\,\alpha/2}{[(\sigma^2_E + \sigma^2_G - \sigma^2_{Px})/n + \sigma^2_{Px}]^{1/2}}$
Polycross family	$\frac{-pq\,\alpha/4}{[(\sigma^2_E + \sigma^2_G - \sigma^2_{Px})/n + \sigma^2_{Px}]^{1/2}}$
Full-sib family	$\frac{-pq\,\alpha/2}{[(\sigma^2_E + \sigma^2_G - \sigma^2_{FS})/n + \sigma^2_{FS}]^{1/2}}$
Selfed family or selfed progeny test	$\frac{-pq\,\alpha}{[(\sigma^2_E + \sigma^2_{S_1} - \sigma^2_{S_1F})/n + \sigma^2_{S_1F}]^{1/2}}$

* $\alpha = (A + 3pD + 3p^2T + p^3F)$, the usual "alpha" for autotetraploid populations (Hill, 1971b). $\alpha' = A + [3p + (q-p)/4]D + \{3p^2 - [p(p-2q)]/2\}T + \{p^3 - [p^2 - (1-4q)]/4 - [pq(1-2q)]/12\}F$ could not be defined in terms of parameters for random mating autotetraploid populations. σ^2_E, σ^2_G, σ^2_{Px}, σ^2_{FS}, $\sigma^2_{S_1}$, $\sigma^2_{S_1F}$ represent environmental variance, total genetic variance, variance due to polycross family means, variance due to full-sib family means, total genetic variance in an S_1 population, and variance due to S_1 family means, respectively. n represents the number of individuals per family.

The denominators of the response equations are similar to those given by Sprague (1966), but the genetic components of variance should be interpreted in terms of autotetraploids (Levings and Dudley, 1963) (Table 2). When other parameters are equal, full-sib family selection should always be slightly less effective than polycross progeny test selection, because σ^2_{FS} is always larger than σ^2_{Px}. An interpretation in terms of autotraploid genetic variances could not be found for the total variance in a selfed population (σ^2_{S1}) or for the variance among selfed family means (σ^2_{S1F}).

Numerical and graphic comparisons of the methods were conducted, because evaluation of the methods

is difficult by examination of the equations alone (Fig. 1). The graphs are coded and interpreted in such a way that the object of selection is to increase gene frequency, or to move from left to right. Thus, the left portion of each of the graphs is of greatest interest because selection would be most likely to be practiced when gene frequency is low.

Response to selection with each methods was always greater when environmental variance was low than when it was high (Fig. 1). As expected, response with individual selection was affected more by changes in environmental variance than was response with the progeny test or family selection methods. The response curves were symmetric when there was no dominance and were skewed to the left or to the right with dominance and recessive models, respectively. Maximum differences between the methods of selection were usually observed in the regions of maximum response to selection.

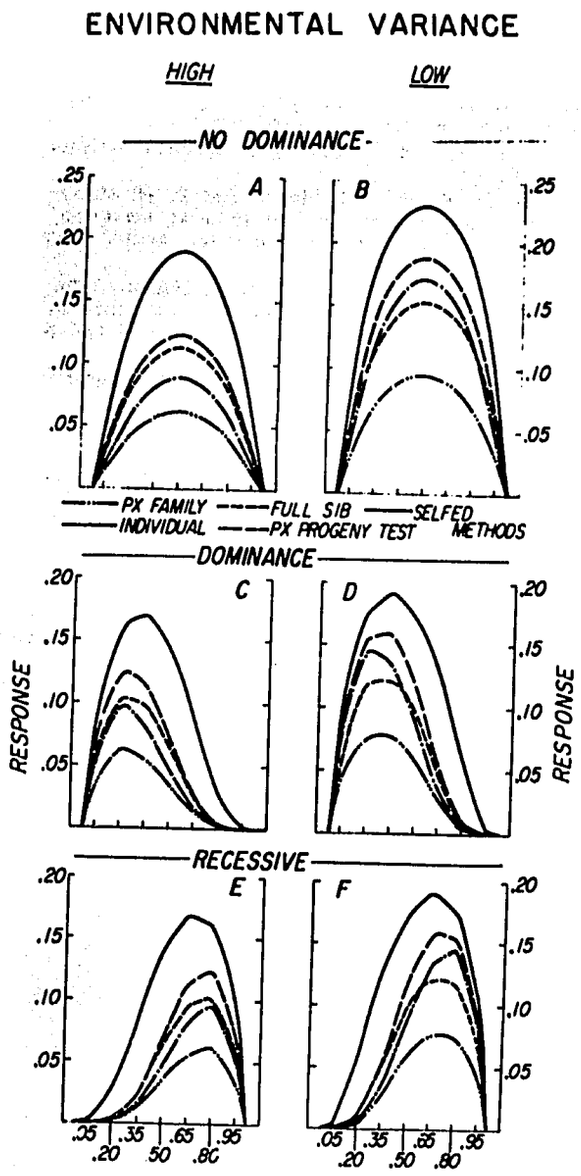

Fig. 1. Response as change in gene frequency (y axis) for different gene frequencies (x axis) with indicated methods of selection for low environmental variance (σ^2_E = 0.0675) and high environmental variance (σ^2_E = 0.5275). Family size is 10 with family and progeny test methods.

The theoretical ranking of the methods of selection when the environmental variance was high was the same with each level of dominance (Fig. 1, A, C, and E). Selfed progeny test and selfed family selection were the most effective, followed by polycross progeny test, full-sib family, individual, and polycross family selection. Differences between the methods were very small at low gene frequencies with no dominance or with complete dominance (Fig. 1, A and 1 C, respectively). Except for polycross progeny test and full-sib family selection, responses diverged greatly at intermediate gene frequencies with no dominance (Fig. 1A). Polycross family and full-sib family selection gave similar responses with complete dominance for gene frequencies between 0 and 0.2 (Fig. 1C). Selfed progeny test and selfed family selection were markedly superior to the other methods for gene frequencies above 0.2 with the dominance model and below 0.8 with the recessive model (Fig. 1, C and E).

Selfed progeny test, selfed family and polycross progeny test selection were the three most effective methods, and polycross family was the least effective method with each of the genetic models when environmental variance was low (Fig. 1, B, D, and F). Full-sib family selection was slightly more effective than individual selection at the extreme gene frequencies with no dominance, but individual selection was superior at intermediate gene frequencies (Fig. 1B). Response with individual selection was similar to that for polycross progeny test selection, and was superior to that for full-sib family selection at low gene frequencies with complete dominance (Fig. 1D). Individual selection maintained its superiority over full-sib family selection until gene frequency was about 0.5. Full-sib family selection was slightly more effective than individual selection at low gene frequencies with the recessive model (Fig. 1F). As was true with high environmental variance, selfed family and selfed progeny test selection were more effective than the other methods at high gene frequencies in the dominance model and at low gene frequencies in the recessive model.

DISCUSSION

The choice of a breeding method should not be made on the basis of the equations and response curves alone. Our comparisons did not consider selection intensity or time per generation, both of which are very important in any selection program. With cross-pollinated, autotetraploid species, no method of selection is likely to achieve a practical level of resistance to diseases or insects in one generation. Thus, the most desirable selection methods for cross-pollinated autotetraploids would permit large selection intensity, have a short generation interval, and be adaptable to a cyclic program.

No method is better than individual selection from the viewpoint of meeting the above three criteria. Selection intensity can be increased at will, generation time can be short, and individual selection is readily adapted to cyclic programs. However, responses with individual selection decreases rapidly as

environmental variance increases and probably will not be effective when environmental variance is very large. If refinement of techniques does not reduce the environmental variance to a level that will permit individual selection to be effective, the breeder has no choice but to use another method.

Family selection is less affected by large environmental variance than individual selection. It can be adapted to cyclic selection, because individuals from the selected families can be used as parents of families for the next cycle. Polycross family selection can be readily adapted to most cross-pollinated, autotetraploid species, but it was always theoretically the least effective method examined. Response with full-sib family selection was similar to that with individual selection in all the cases we studied. Selfed family selection was the most effective of the family methods, but it cannot be used for more than one or two generations in most cross-pollinated, autotetraploid forage species without the undesirable side effects of inbreeding, and self-incompatibility in many of these species severely limits the use of selfed family selection. Alternating selfed family selection with another method will not eliminate the inbreeding, because part of any accumulated inbreeding would be transmitted from parent to offspring in autotetraploids (Busbice, 1969). Thus, we concluded that full-sib family selection was the most promising of the family selection methods, but it would be recommended over individual selection only when environmental variance was extremely large.

When selection intensity and generation time were ignored, progeny test methods were always the most effective. However, progeny test selection must always operate at a lower selection intensity than individual selection, and an extra generation is required between cycles of selection. When individual gene frequencies are extremely low, selfed or polycross progny test selection would be useful to increase gene frequency to a value for which individual selection would be effective. If the desired genotype was a recessive homozygote, selfed progeny test selection would be much more effective than polycross progeny test selection.

The digenic effect never occurred in our response equations, indicating that digenic effects may have no role in change in gene frequency in autotetraploids. The deviations from simple α with selfed progeny test and selfed family selection were caused by destruction of the random-mating equilibrium properties of the population, and did not indicate that digenic effects per se were responsible for changes in gene frequency. The equation proposed by Levings and Dudley (1963) for heritability in autotetraploids contained the digenic component, indicating that digenic variance could have a role in change in the population mean. Selection in autotetraploids destroys the random-mating equilibrium, and once selection is relaxed, the mean changes until a new equilibrium is reached (Hill, 1971a). We offer the conjecture that the magnitude of the shift to a new equilibrium after selection is relaxed is proportional to the magnitude of the digenic variance, but we have no proof of this at the present time.

REFERENCES

Allard. R. W. 1960. Principles of plant breeding. John Wiley and Sons, Inc., New York. 485 p.

Busbice, T. H. 1969. Inbreeding in synthetic varieties. Crop Sci. 9:601-604.

Comstock, R. E., H. F. Robinson, and P. H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. J. 41:360-367.

Dudley, J. W., R. R. Hill, Jr., and C. H. Hanson. 1963. Effects of seven cycles of recurrent phenotypic selection on means and genetic variances of several characters in two pools of alfalfa germplasm. Crop Sci. 3:543-546.

Falconer, D. S. 1960. Introduction to quantitative genetics. The Ronald Press Co., New York. 365 p.

Hill, R. R., Jr. 1971a. Selection in autotetraploids. Theor. Appl. Genet. 41:181-186.

———. 1971b. Effect of the number of parents on the mean and variance of synthetic varieties. Crop Sci. 11:283-286.

Levings, C. S., III, and J. W. Dudley. 1963. Evaluation of certain mating designs for estimation of genetic variance in autotetraploid alfalfa. Crop Sci. 3:532-535.

Robertson, A. 1963. Discussion: some comments on quantitative genetic theories. p. 108-115. *In* W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. NAS-NRC Publ. 982.

Sprague, G. F. 1966. Quantitative genetics in plant improvement. p. 315-354. *In* Kenneth J. Frey (ed.) Plant breeding—a symposium held at Iowa State University. Iowa State University Press, Ames.