THEORETICAL GAINS FOR DIFFERENT POPULATION IMPROVEMENT PROCEDURES

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CONTENTS

Theoretical Gains For Different Population Improvement Procedures

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SUMMARY

An understanding of the derivations of the expected genetic advance for different selection schemes should enable plant breeders to choose the most efficient method to use in a given problem, and to make necessary modifications to improve their efficiency.

This publication shows in simple mathematics the step by step derivation of eight intrapopulation selection schemes used in the improvement of population means, and five inter-population selection methods for the improvement of variety crosses.

Most of these methods had been derived before, individually or in groups, in various notations, thereby making their comparison difficult for persons with inadequate statistical backgrounds. This information should be useful to plant breeding students and teachers.

The intra-population selection schemes described are mass 1 (control of two parents), mass 2 (control of one parent), S_1, half-sib, full-sib, modified ear-to-row, testcrossing and reciprocal full-sib.

Based on the ratio of the amount of additive genetic variance to the number of generations per cycle, the most efficient methods are mass 1, mass 2, modified ear-to-row and S_1 testing, respectively. However, other factors such as the number of growing seasons in a locality, heritability of the character and breeding objectives could be an overriding factor in the choice of a selection scheme.

The inter-population selection schemes discussed are testcrossing using one of the intended pair as the tester, testcrossing both populations to a common tester, reciprocal half or full-sib selection and the use of populations developed by S_1 progeny testing. Of the above inter-population methods reciprocal full-sib selection offers the most efficient way of extracting hybrids and simultaneous improvement of the individual populations.

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INTRODUCTION

The future success of the inbred-hybrid system in maize rests on the improvement of the population or populations from which the inbreds are derived. Population improvement methods currently in use can be divided into intra-population selection schemes where the objective is the improvement of the population mean, and inter-population selection schemes where improvement of the variety cross is the desired goal.

Sprague (1967) summarized the rates of progress expected in intra-population improvement using mass, half-sib, full-sib and S_1 progeny selection.

Comstock, Robinson and Harvey (1949) compared three inter-population selection methods in which the target population is the variety cross.

Most of the methods that we will present have been derived before, either individually or in groups, in various notations, thereby making comparisons of their efficiency difficult for persons with inadequate statistical backgrounds. Likewise, prediction equations given in textbooks are generally for mass selection as practiced in animal breeding which is inadequate as an illustration of the various selection methods now used by plant breeders.

This publication will clarify and illustrate how the components of genetic advance were derived for the above-mentioned inter- and intra-population schemes and also for some additional schemes or variations of the above schemes.

ASSUMPTIONS AND DESCRIPTION OF THE BASE POPULATION

In all situations, we will consider only random mating base populations that are in equilibrium which might be exemplified by an open-pollinated corn variety. Furthermore, for simplicity of the mathematics involved, we will assume diploid pairing at meiosis, independent assortment of genes (no linkage), no multiple alleles and no epistasis.

The genotypic array, relative genotypic frequencies and values, and frequency of the favorable allele in the base population are shown in the first four columns of Table 1. Such a population will have a genotypic mean of:

$$\overline{g}_1 = \sum_{i=1}^{n} [(p_i - q_i) a_i + 2p_i q_i h_i]$$

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where 2a is the difference between the two homozygotes and h is the deviation of the heterozygote from mid-parental value. The genotypic variance is:

$$\sigma^2_{g_1} = \sum_{i=1}^{n} (p_i^2 a_i^2 + 2p_i q_i h_i^2 + q_i^2 a_i^2)$$

where the summation over i includes the sum of the effects of all n loci affecting the character. The genotypic variance can be partitioned into two components, a part due to the linear regression of the genotype on the number of favorable alleles (additive genetic variance), and deviations from regression which under our assumptions represents dominance variance. The two variances are obtained as follows:

Additive genetic variance (σ^2_a) = $(Cov \; p_1 g_1)^2 / \sigma^2_{p_1}$

$$= \frac{\{p^2 a + 2pqh(1/2) - \bar{p}[(p-q)a + 2pqh]\}^2}{p^2 + 2pq(1/4) - (\bar{p})^2}$$

where $\bar{p} = p$ is the mean frequency of the favorable allele. Summing over all loci we get the expression for

$$\sigma^2_a = \sum_{i=1}^{n} 2p_i q_i [a_i + (q_i - p_i)h_i]^2$$

Dominance variance (σ^2_d) is obtained as the difference between $\sigma^2_{g_1}$ and

σ^2_a or $\sigma^2_d = \sigma^2_g - \sigma^2_a = 4\sum_{i=1}^{n} (p_i q_i h_i)^2$, for the trait under

consideration.

POPULATION CHANGES UNDER ARTIFICIAL SELECTION

Falconer (1960) discussed the general changes in the genetic properties of a population when a breeder chooses the parents and mating design to bring about the next generation. We can summarize the changes that affect the population mean as follows:

1. Selection of superior parents for the next generation results in a change in gene frequency.

2. The change in gene frequency will bring about a change in mean genotypic value in the next generation.

3. The product of a and b is the expected change in the population mean from one generation to the next.

Falconer (1960) showed that the change in gene frequency $(\triangle p_i)$ at a locus is:

$\triangle p_i = S\beta p_i g_i$; where S is the selection differential (phenotypic superiority) and

$\beta p_i g_i$ = regression of the gene frequency on genotypic value
$= \text{Cov } p_i g_i / \sigma_{g_1}^2$

therefore, genetic progress $(\triangle g_i)$ at a locus is given by the equation

$$\triangle g_i = \frac{S \text{ cov } p_i g_i}{\sigma_{g_1}^2} \frac{\delta \bar{g}_i}{\delta p_i}$$

which is the product of the change in gene frequency and the change in mean genotypic value per unit change in gene frequency. This is the basic equation used to compute expected progress for all intra-population selection schemes.

GENETIC PROGRESS EXPECTED FROM INTRA-POPULATION SELECTION SCHEMES

1. *Mass selection*—Individuals are selected based upon their pheno-type. Selected individuals are then random mated to produce the next generation.

Since $\triangle g_i = (\triangle p_i) \delta \bar{g}_i / \delta p_i$, for a particular locus

$$\text{cov } p_1 g_1 = p^2 a + 2pqh(1/2) - \bar{p}\bar{g}_1$$

$$= (p^2 - p^2 + pq)a + (pq - 2p^2 q)h$$

$$= pq [a + (q-p)h]$$

and $\delta \bar{g}/\delta p = \dfrac{\delta}{\delta p} [(p-q)a + 2pqh]$

$$= 2[a + (q-p)h]$$

which is the expression for the change in mean genotypic value per unit change in gene frequency for all intra-population schemes described in this paper. Therefore the increase in population mean $(\triangle g_{M(1)})$ due to the combined effects of all loci affecting the trait is:

$$\triangle g_{M(1)} = \frac{S}{\sigma_{p_m}^2} \sum_{i=1}^{n} 2p_i q_i [a_i + (q_i - p_i)h_i]^2$$

where σp_m^2 is the total phenotypic variance of the population and S is the selection differential previously mentioned.

For traits like yield in cross fertilizing crops such as corn, random mating will have already taken place before selections are made. The ears selected have half-sib seed and the effective gene frequency of the favorable allele in the genotype changes from values of Col. 4 to values in Col. 6 as shown in Table 1 under the heading of mass selection 2. Therefore the covariance between genotype and gene frequency for mass selection 2 is:

$$\text{Cov } p_2 g_1 = p^2 a(1/2) + 2pqh(1/4) - \bar{p}\,\bar{g}_1$$

$$= pq\,[a + (q-p)h]/2$$

so that genetic advance ($\Delta g_{M(2)}$) is:

$$\Delta g_{M(2)} = \frac{S}{\sigma_{p_m}^2} \sum_{i=1}^{n} p_i q_i\,[a_i + (q_i - p_i)h_i]^2$$

which is half as much as $\Delta g_{M(1)}$.

2. S_1 *progeny selection*—A random sample of plants in the base population are selfed. Self progenies are evaluated in a yield trial and plants of superior S_1 families or superior individuals themselves are random mated to produce the next generation. Using the information in Table 1 the covariance needed to compute Δp_i is:

$$\text{Cov } p_1 g_3 = p^2 a + 2pq\,(h/2)(1/2) - \bar{p}_1 \bar{g}_3$$

$$= pq\,[a + h(q-p) + h(p-1/2)]$$

$$= pq\,[\alpha + (p-1/2)h]$$

where $\bar{g}_3 = (p\text{-}q) + pqh$ is the mean genotypic value of the S_1 progenies, and $\alpha = [a + (q\text{-}p)h]$ is the average effect of substituting allele "B" for "b." Therefore the change in the population (Δg_s) using S_1 progeny selection is:

$$\Delta g_s = \frac{S}{\sigma_{p_s}^2} \sum_{i=1}^{n} p_i q_i\,[\alpha_i + (p_i - 1/2)\,h_i]\,[2\alpha_i]$$

$$= \frac{S}{\sigma_{p_s}^2} \sum_{i=1}^{n} 2p_i q_i\,[\alpha_i^2 + (p_i - 1/2)\,h_i \alpha_i].$$

The prediction equation for S_1 testing contains all of the additive genetic variance in the base population plus a component which is mainly a function of degree of dominance.

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3. *Full-sib family selection*—Individuals of superior full-sib families are random mated to produce the next generation. The pertinent covariance relationship is between the mean genotypic value (g_4) and frequencies of the favorable allele (p_4) in the full-sib progenies (Table 1). Thus

$$
\begin{aligned}
\text{Cov } p_4 g_4 &= p^4 a + 2p^3 q[(a + h)/2](3/4) + p^2 q^2 h(1/2) \\
&\quad + 2p^3 q[(a + h)/2](3/4) + 4p^2 q^2 (h/2)(1/2) \\
&\quad + 2pq^3[(h - a)/2](1/4) + p^2 q^2 h\ (1/2) \\
&\quad + 2pq^3[h - a)/2](1/4) - \overline{p_4}\,\overline{g_4} \\
&= \frac{pq}{2}\ [a + (3p^2 + 4p - 4p^2 + 1 - 2p + p^2 - 4p)h] \\
&= \frac{pq}{2}\ [a + (q-p)h]
\end{aligned}
$$

where $\overline{p}_4 = p$ and $\overline{g}_4 = [(p\text{-}q)a + 2pqh]$ are the expected values of p_4 and g_4, respectively. Therefore genetic progress for full-sib selection (Δg_{FS}) is:

$$
\Delta g_{FS} = \frac{S}{\sigma^2_{p_{fs}}} \sum_{i=1}^{n} p_i q_i\ [a_i + (q_i - p_i)h_i]^2 .
$$

4. *Half-sib progeny selection*—Random individuals are chosen and each is mated to a different set of randomly chosen individuals. Performance of half-sib families is the basis of selection (selection criterion). Two types of selection units (genotypes to be random mated) could be used which differ in their expected genetic progress. We will designate as Case 1 the situation in which individuals of superior families are the selection units. In Case 2, the selection unit is the self-progeny of the common parent of superior half-sib progenies. If maternal effects influence the character studied, the common parent should be used as males.

For Case 1 the covariance between the mean genotypic value (g_5) and frequency of favorable allele (p_5) in the half-sib progenies determines Δp_i. The expected value of g_5 and p_5 are:

$$
\begin{aligned}
E(g_5) = \overline{g}_5 &= p^2(pa + qh) + 2pq[(p\text{-}q)\ a + h]/2 \\
&\quad + q^2(ph\text{-}qa) \\
&= (p\text{-}q)\ a + 2pqh
\end{aligned}
$$

$$
E(p_5) = \overline{p}_5 = p^2(1/2) + 2pq(1/4) = p/2 .
$$

Therefore

$$\text{Cov } p_5 g_5 = p^2(pa + qh)(1/2)$$
$$+ 2pq\{[(p-q)\,a + h]/2\}(1/4) - \bar{p}_5\bar{g}_5$$
$$= (p/4)(2p^2 + pq - q^2 - 2p + 2q)a$$
$$+ (pq/4)(2p + 1 - 4p)h$$
$$= (pq/4)[a + (q-p)h]$$

and genetic gain $(\Delta g_{HS(1)})$ for Case 1 is:

$$\Delta g_{HS(1)} = \frac{S}{\sigma^2_{P_{hs}}} \sum_{i=1}^{n} (1/2)p_i q_i \,[a_i + (q_i - p_i)h_i]^2.$$

In Case 2 the pertinent covariance is between the genotypic value of the half-sib progenies and the frequency of the favorable alleles in the base population such that:

$$\text{Cov } p_1 g_5 = p^2(pa + qh) + 2pq\{[(p-q)\,a$$
$$+ h]/2\}(1/2) - \bar{p}_1\bar{g}_5$$
$$= pq\,[a + (q-p)h]$$

so that genetic gain for Case 2 $(\Delta g_{HS(2)})$ is:

$$\Delta g_{HS(2)} = \frac{S}{\sigma^2_{P_{hs}}} \sum_{i=1}^{n} p_i q_i [a_i + (q_i - p_i)h_i]^2.$$

If the selection differential and phenotypic variance are the same, then twice as much gain is expected when self progenies of the superior male parents are intermated compared to intermating the superior half-sib families themselves.

5. *Modified ear-to-row*—This method, which combines half-sib testing and mass selection within superior half-sib progenies, was described by Webel and Lonnquist (1967). The family selection portion is essentially the same as half-sib testing except that instead of recombining selected progenies, they are pollinated by bulk pollen from both unselected and selected progenies. Therefore, the effective frequency of the favorable alleles in the half-sib progenies will be one-half (see p_6 under modified ear-to-row in Table 1) of that available if only selected progenies were intermated. To get Δp_i the needed covariance is:

$$\text{Cov } p_6 g_5 = p^2(pa + qh)(1/4)$$
$$+ 2pq\{[(p - q)a + h]/2\}(1/8) - \overline{p}_6\overline{g}_5$$
$$= (p/8) [2p(p - 1) + q(p-q) + 2q]a$$
$$+ (pq/8)(q-p)h$$
$$= (pq/8)[a + (q-p)h]$$

where $\overline{p}_6 = p/4$ is the expected value of p_6 and $\overline{g}_5$ is the same as in half-sib selection. Consequently, the genetic progress in the half-sib portion ($\triangle g_1$) is:

$$\triangle g_1 = \frac{S}{\sigma^2_{P_{hs}}} \sum_{i=1}^{n} (1/4) p_i q_i [a_i + (q_i - p_i) h_i]^2.$$

After the superior half-sib progenies are identified (the "among half-sib" portion of the gain) the best plants within each progeny are selected. The change in gene frequency is therefore determined by the covariance between genotypes within half-sib progenies and their effective frequencies of favorable alleles. The frequencies of favorable alleles in the genotype within half-sib families are shown in p_7 (Table 1). However, as in mass selection 2, the pollen comes at random from the whole population so that the effective frequency of the favorables alleles are again reduced by one-half as shown in Col. p_8 (Table 1). The desired covariance is:

$$\text{Cov } p_8 g_8 = p^2[pa (1/2) + qh (1/4) - \overline{g}_8\overline{p}_8]$$
$$+ 2pq [(pa/2)(1/2) + (h/2) (1/4) - \hat{g}_8\hat{p}_8]$$
$$+ q^2[ph(1/4) - \tilde{g}_8\tilde{p}_8]$$
$$= (pq/8)(2p^2 + 3p - 2p^2 + q + 2pq + 2q^2)a$$
$$+ (pq/8)(3-6p)h$$
$$= (3pq/8)[a + (q-p)h]$$

where $\overline{g}_8 = pa + qh$, $\hat{g}_8 = (pa + h - qa)/2$

and $\tilde{g}_8 = ph - qa$ are the mean genotypic values within half-sib progenies for base population genotypes BB, Bb and bb, respectively; and $\overline{p}_8 = \frac{1+p}{4}$, $\hat{p}_8 = \frac{1+2p}{8}$ and $\tilde{p}_8 = p/4$ are the corresponding mean frequencies of the favorable allele in the above half-sib progenies. Therefore the expected progress ($\triangle_{g2}$) in doing mass selection within the selected half-sib progenies is:

$$\Delta g_2 = \frac{S}{\sigma^2_{P_{fs}}} \sum_{i=1}^{n} (3/4) p_i q_i [a_i + (q_i - p_i) h_i]^2$$

giving a combined gain (Δg_{ER}) for modified ear-to-row selection of:

$$\Delta g_{ER} = \Delta g_1 + \Delta g_2$$

$$= \frac{S}{\sigma^2_{P_{hs}}} \sum_{i=1}^{n} (1/4) p_i q_i [a_i + (q_i - p_i) h_i]^2$$

$$+ \frac{S}{\sigma^2_{P_{fs}}} \sum_{i=1}^{n} (3/4) p_i q_i [a_i + (q_i - p_i) h_i]^2.$$

INTRA-POPULATION IMPROVEMENT USING ANOTHER POPULATION AS TESTER

1. *Topcross progeny selection*—In this method half-sib progenies between population A (population to be improved) and the tester are the selection criterion. The self progenies of the selected parents are the selection units. Let "r" be the frequency of "B" and "s = 1 − r" be the frequency of "b" in the tester parent. To compute the change in gene frequency due to selection we can use the mean genotypic values of half-sib progenies (g_5) in Table 1 with the condition that for p we substitute r and for q we use s. Clearly this method reduces to half-sib testing as previously described when p = r. Consequently, the needed covariance is:

$$\text{Cov } p_1 g_5 = p^2 (ra + sh)$$

$$+ 2pq(1/2)[(r-s) a + h] (1/2) - \overline{p}_1 \hat{g}_5$$

$$= (pq/2)(r + s)a$$

$$+ [p^2 (s - 1 + r) + pq (1/2 - r)] h$$

$$= (pq/2)[a + (s - r) h]$$

where $\hat{g}_5 = (pr - qs)a + [p + r(q - p)h]$ is the mean of the testcross population. Therefore, genetic gain (Δg_{TC}) using topcross progeny selection is:

$$\Delta g_{TC} = \frac{S}{\sigma^2_{P_{hs}}} \sum_{i=1}^{n} \frac{p_i q_i}{2} \alpha_i^{T}(2\alpha_i^{A})$$

$$= \frac{S}{\sigma^2_{P_{hs}}} \sum_{i=1}^{n} p_i q_i \, \alpha_i^{A}\alpha_i^{T}$$

where α_i^{A} and α_i^{T} are the average effect of gene substitution at the ith locus for populations A and T, respectively.

2. *Reciprocal full-sib family selection*—This method was described by Hallauer and Eberhart (1970) and Jones, Compton and Gardner (1971). It is mainly used as an inter-population selection method but has also been mentioned by the above workers to be effective in improving the means of populations involved in variety crosses.

Therefore, we would like to show how the means of the two populations involved in the variety cross change under a reciprocal full-sib selection scheme. The selection units are the self-progenies of the selected parents, and the selection criteria are the full-sib families between the two populations.

To derive the pertinent covariance determining the change in gene frequencies in the two populations we can use the information in the full-sib column of Table 1. However the frequency of genotypes for parent 2 should be changed into "r" and "s" to generalize the expression since gene frequencies may differ in the two populations.

$$\begin{aligned}
\text{Cov } p_1 g_4 &= \{p^2[r^2 a + 2rs(a + h)/2 + s^2 h] \\
&+ 2pg(1/2)[r^2(a + h)/2 + 2rs(h/2) \\
&+ s^2(h - a)/2] - \overline{p}_1\overline{g}_4\} \\
&= (pq/2)[(r^2 - s^2 + 2s)a \\
&+ (r^2 + 2rs + s^2 - 2r)\,h] \\
&= (pq/2)[a + (s - r)h].
\end{aligned}$$

If we let $\alpha^A = [a + (q - p)h]$ and $\alpha^B = [a + (s - r)h]$,

then $\displaystyle \Delta g_{RFS(A)} = \frac{S}{\sigma^2_{P_{fs}}} \sum_{i=1}^{n} \frac{p_i q_i}{2} \, \alpha_i^{B}(2\alpha_i^{A})$

$$= \frac{S}{\sigma^2_{P_{fs}}} \sum_{i=1}^{n} p_i q_i \alpha_i^{A}\alpha_i^{B}$$

and $\Delta\text{RFS(B)} = \dfrac{S}{\sigma^2_{P_{fs}}} \sum\limits_{i=1}^{n} r_i s_i \alpha_i^B \alpha_i^A.$

IMPROVEMENT OF THE VARIETY CROSS

The cross between two random mating populations where the frequency of "B" is "p" and "r" for populations A and B, respectively; and where the frequencies of "b" in the two populations are $q = 1 - p$ and $s = 1 - r$ will have a mean of:

$$\overline{X}_{AxB} = (p + r - 1)a + (p + r - 2pr)h.$$

After selection changes gene frequencies the new cross mean is:

$$\overline{X}'_{AxB} = [(p + \Delta p) + (r + \Delta r) - 1]a + [(p + \Delta p) + (r + \Delta r) - 2(p + \Delta p)(r + \Delta r)]h$$

therefore, the change in the cross mean is:

$$\Delta\overline{X} = \overline{X}'_{AxB} - \overline{X}_{AxB} = (\Delta p + \Delta r)a + (\Delta p + \Delta r - 2r\Delta p - 2p\Delta r)h_j$$

disregarding the product $\Delta p \Delta r$ as being small.

Current techniques used in inter-population improvement, where the target population is the variety cross, may be divided into the following 4 methods:

Method I. Topcrossing to a tester—The tester may or may not be one of the parental varieties of the desired variety cross.

Method II. Topcrossing populations A and B to a common tester or tester series but the target population is the AxB cross.

Method III. Reciprocal recurrent selection on populations A and B where each is the tester for the other.

Method IV (a). Intra-population S_1 testing on one population.
  (b). Intra-population S_1 testing on both populations.

Following the procedures in the intra-population section the expressions for Δp in the four methods are:

$$\Delta p_I = \dfrac{S}{\sigma^2_{P_{hs}}} \, pq\alpha^T \qquad\qquad \Delta p_{III} = \dfrac{S}{\sigma^2_{P_{hs\ or\ fs}}} \, pq\alpha^B$$

$$\Delta p_{II} = \text{same as } \Delta p_I \qquad\qquad \Delta r_{III} = \dfrac{S}{\sigma^2_{P_{hs\ or\ fs}}} \, rs\alpha^A$$

$$\Delta r_{II} = \dfrac{S}{\sigma^2_{P_{hs}}} \, rs\alpha^T$$

Table 1. Pertinent information needed to determine parameters of the base population and to quantify genetic progress under different selection schemes.

Characteristic of base population				Mass selection 2		S_1 selection		Full-sib selection			
Geno-types (Z)	Freq. of Z	g_1*	p_1†	δ p_2	coded p_2	Self progenies Genotype	g_3¶	Parent 2 Genotype (W)	Freq. of W	g_4‖	p_4**
BB	p^2	a	1	$\frac{1+p}{2}$	1/2	BB	a	BB	p^2	a	1
								Bb	2pq	(a+h)/2	3/4
								bb	q^2	h	1/2
Bb	2pq	h	1/2	$\frac{1+2p}{4}$	1/4	BB	a/4	BB	p^2	(a+h)/2	3/4
						Bb	h/a $\left.\right\}\frac{h}{a}$	Bb	2pq	h/2	1/2
						bb	-a/4	bb	q^2	(h-a)/2	1/4
bb	q^2	-a	0	$\frac{p}{2}$	0	bb	-a	BB	p^2	h	1/2
								Bb	2pq	(h-a)/2	1/4
								bb	q^2	-a	0

Half-sib selection					Modified ear-to-row selection					
Half-sib Geno-type (Y)	Progenies freq. of Y	g_5††	p_5 $\delta\delta$	coded p_5	p_6 ¶¶	coded p_6	p_7 ‖ ‖	g_8***	p_8 †††	coded p_8
BB	p	pa+qh	$\frac{1+p}{2}$	1/2	$\frac{1+3p}{4}$	1/4	1	pa	$\frac{1+p}{2}$	1/2
Bb	q						1/2	qh	$\frac{1+2p}{4}$	1/4
BB	p/2	$\frac{[(p-q)a+h]}{2}$	$\frac{1+2p}{4}$	1/4	$\frac{1+6p}{8}$	1/8	1	pa/2	$\frac{1+p}{2}$	1/2
Bb	1/2						1/2	h/2	$\frac{1+2p}{4}$	1/4
bb	q/2						0	-qa/2	p/2	0
Bb	p	ph-qa	p/2	0	$\frac{3p}{4}$	0	1/2	ph	$\frac{1+2p}{4}$	1/4
bb	q						0	-qa	p/2	0

* Coded mean genotypic value 2a is the difference between the two homozygotes, h is the deviation of the heterozygote from mid-parental value.

† Frequency of favorable allele in the genotype.

δ Effective frequency of favorable allele; mean of p_1 and p.

¶ Frequency of favorable allele in the self-progenies.

‖, ** Mean genotypic value and frequency of favorable allele in the full-sib progenies, respectively.

††, $\delta\delta$ Mean genotypic value and frequency of favorable allele in the half-sib progenies, respectively.

¶¶ Frequency of favorable allele in half-sib progenies; mean of p_6 and p.

‖ ‖, *** Frequency of favorable allele and mean value of genotypes within half-sib families.

††† Effective frequency of favorable alleles on genotypes within half-sib families; mean of p_7 and p.

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$$\Delta p_{IV(a)} = \frac{S}{\sigma^2_{P_s}} pq \, [\alpha^A + (p - 1/2)h]$$

$$\Delta p_{IV(b)} = \text{same as in IV(a)}$$

$$\Delta r_{IV(b)} = \frac{S}{\sigma^2_{P_s}} rs [\alpha^B + (r - 1/2)h]$$

where α^A, α^B and α^T are the effects of gene substitution in populations A, B and the tester.

Substituting the above expressions for Δp into the formula for $\Delta \overline{X}$ will give the expected genetic progress (ΔG) in the variety cross under each selection method (Table 2).

COMPONENTS OF PHENOTYPIC VARIATION

The components of phenotypic variation for all selection methods could be grouped into σ^2 (environmental variation), σ^2_H (total hereditary variation) and the identifiable genetic component of variation. σ^2 could further be subdivided into (σ^2_W) environmental variation between plants in an experimental unit and (σ^2_e) experimental error due to replications. The identifiable genetic components that we will consider are σ^2_m, σ^2_F and σ^2_S which are the variances among half-sib, full-sib and S_1 progenies. The phenotypic variances in the different selection schemes could then be written as:

$$\sigma^2_{P_m} = \sigma^2 + \sigma^2_H$$

$$\sigma^2_{P_{hs}} = \frac{(\sigma^2_W + \sigma^2_H - \sigma^2_m)}{rm} + \frac{\sigma^2_e}{r} + \sigma^2_m$$

$$\sigma^2_{P_{fs}} = \frac{(\sigma^2_W + \sigma^2_H - \sigma^2_F)}{rm} + \frac{\sigma^2_e}{r} + \sigma^2_F$$

$$\sigma^2_{P_S} = \frac{(\sigma^2 + \sigma^2_H - \sigma^2_S)}{rm} + \frac{\sigma^2_e}{r} + \sigma^2_S$$

where r and m are the number of replicates and plants within an experimental unit, respectively.

Table 2. Expected genetic progress and number of generations per cycle of different intra- and inter-population selection schemes.

Selection method	Expected genetic progress[*]	Generations per cycle (N)
A. Intra-population schemes		
1. Mass selection (1)	$\Delta g_{M(1)} = \dfrac{K\sigma^2_a}{\sigma_{P_m}}$	1
2. Mass selection (2)	$\Delta g_{M(2)} = \dfrac{K(1/2)\sigma^2_a}{\sigma_{P_m}}$	1
3. S_1 progeny test	$\Delta g_S^+ = \dfrac{K(\sigma^2_a + C)}{\sigma_{P_s}}$	3
4. Full-sib test	$\Delta g_{FS} = \dfrac{K(1/2)\sigma^2_a}{\sigma_{P_{fs}}}$	2
5. Half-sib test (1)	$\Delta g_{HS(1)} = \dfrac{K(1/4)\sigma^2_a}{\sigma_{P_{hs}}}$	2
6. Half-sib test (2)	$\Delta g_{HS(2)} = \dfrac{K(1/2)\sigma^2_a}{\sigma_{P_{hs}}}$	3

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Table 2. (continued)

Selection method	Expected genetic progress[*]	Generations per cycle (N)
7. Modified ear to row selection	$\Delta g_{ER} = \dfrac{K(1/8)}{\sigma_{P_{hs}}} \sigma^2{}_a + \dfrac{K(3/8)}{\sigma_{P_{fs}}} \sigma^2{}_a$	1
B. Intra-population improvement with another tester population		
1. Top crossing	$\Delta g_{TC} = \dfrac{K}{\sigma_{P_{hs}}} \sum\limits_{i=1}^{n} p_i q_i \alpha_i{}^{T} \alpha_i{}^{A}$	3
2. Reciprocal full-sib family selection	$\Delta g_{RFS} = \dfrac{K}{\sigma_{P_{fs}}} \sum\limits_{i=1}^{n} p_i q_i \alpha_i{}^{A} \alpha_i{}^{B}$	3
C. Improvement of the variety cross		
1. Topcrossing on population to a tester	$\Delta G_I = \dfrac{K(1/2)}{\sigma_{P_{hs}}} \sum\limits_{i=1}^{n} p_i q_i \alpha_i{}^{T} \alpha_i{}^{B}$	3
2. Topcrossing both populations to a common tester	$\Delta G_{II} = \dfrac{K(1/2)}{\sigma_{P_{hs}}} \left(\sum\limits_{i=1}^{n} p_i q_i \alpha_i{}^{T} \alpha_i{}^{B} + \sum\limits_{i=1}^{n} r_i s_i \alpha_i{}^{T} \alpha_i{}^{A} \right)$	3

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Table 2. (continued)

Selection method	Expected genetic progress[*]	Generations per cycle (N)
3. Reciprocal recurrent selection	$\Delta G_{III} = \dfrac{K(1/2)}{\sigma_{P_{hs\ or\ fs}}} \left[\sum_{i=1}^{n} p_i q_i (\alpha_i^B)^2 + \sum_{i=1}^{n} r_i s_i (\alpha_i^A)^2 \right]$	3
4. S_1 testing in one population	$\Delta G_{IV(a)} = \dfrac{K}{\sigma_{P_s}} \sum_{i=1}^{n} p_i q_i \left[\alpha_i^A \alpha_i^T + (p_i - 1/2)\, h\alpha_i^T \right]$	3
5. S_1 testing in both populations	$\Delta G_{IV(b)} = \dfrac{K}{\sigma_{P_s}} \left[\sum_{i=1}^{n} p_i q_i \alpha_i^A \alpha_i^B + \sum_{i=1}^{n} r_i s_i \alpha_i^B \alpha_i^A + \sum_{i=1}^{n} pq(p-1/2) h\alpha^B \right.$ $\left. + \sum_{i=1}^{n} rs(r-1/2) h\alpha^A \right]$	3

*K = selection differential in standard units; σ^2_a = additive genetic variance; σ_{P_m}, $\sigma_{P_{hs}}$, $\sigma_{P_{fs}}$, σ_{P_s} are the phenotypic standard deviations for mass, half-sib, full-sib and self progenies respectively; α_i^A, α_i^B, α_i^T are the effects of gene substitution in populations A, B and the tester, respectively.

+C = $\sum_{i=1}^{n} 2\, p_i q_i (p_i - 1/2)\, h_i [a_i + (q_i - p_i) h_i]$

DISCUSSION

Genetic progress in intra-population selection schemes can be expressed conveniently in terms of the additive genetic variance of the base population (Table 2). Theoretically, these estimates are good for only one cycle since the properties of the population change with selection. However, Kojima and Kelleher (1963), working on *Drosophila pseudoobscura*, found parameters of base populations adequate in predicting response in the first few cycles of selection.

The choice of which intra-population scheme to use depends on many factors. A crude guide is the ratio of the amount of additive genetic variance in the numerator of the formula for expected progress and the number of generations per cycle.

Using the information in Table 2, mass selection 1 has the highest ratio followed by mass selection 2 and modified ear-to-row and S_1 testing, respectively. Some other advantages of mass selection are its simplicity and inexpensiveness.

Using grids to reduce environmental variation between plants, Gardner (1969) reported 2.93% gain per year in 10 cycles of mass selection in the corn variety Hays Golden. On the other hand, Hallauer and Sears (1969), using the grid system, failed to obtain significant gains in yield of corn varieties Krug and Iowa Ideal.

Eberhart (1969) observed that in Kitale, Kenya, at most three generations are possible in two years because of high altitude and long growing season. In this situation, S_1 testing which normally takes three generations might be more efficient than mass selection especially if additive genetic variance is hard to utilize in the latter method due to problems in field husbandry.

However, if over-dominance is the prevalent gene action, this method will suffer most in efficiency compared to other methods of intra-population improvement discussed. This is because the prediction equation contains some expressions besides σ^2_a which are functions of the degree of dominance. Similarly, when a place allows two seasons per year or when a winter nursery is available, full-sib and half-sib testing might be the best choices among the methods.

Preference of family selection methods over mass selection arose because of the difficulty in determining the genetic worth of an individual, and low heritabilities of desired traits. All family selection schemes except modified ear-to-row capitalize on the between family variance which, with the exception of S_1 testing, utilizes less of the additive genetic variance available in the base population than mass selection. Modified ear-to-row uses one-half of the additive genetic variance and requires only one generation per cycle and therefore is as desirable as mass selection 2 for cross-fertilizing crops. Webel and Lonnquist (1967) reported an average of 9.44% yield increase in the corn variety Hays Golden using modified ear-to-row method. They

concluded that modified ear-to-row is a more effective selection method than mass selection. Open pollination of selected families as described by Webel and Lonnquist permits the completion of a cycle each year; however, expected genetic gain is only one-half that expected if the selected families were recombined. On the other hand, since the recombination phase requires an extra year, the expected gain per year is the same.

Theoretically the combination of family and within family selection should bring more rapid genetic progress and should be the best method to use. Selection within families could also easily be incorporated into half-sib (2) and S_1 testing schemes. Falconer (1960) gave the following guide in determining the distribution of the additive genetic variance in combined selection schemes:

$$\sigma^2_{a_I} = r \ \sigma^2_{a_F} + (1 - r) \ \sigma^2_{a_W}$$

values; $\sigma^2_{a_I}$ is the total amount of additive genetic variance available if individual plant selection is used; r is the correlation of breeding values; $\sigma^2_{a_F}$ and $\sigma^2_{a_W}$ the distribution of $\sigma^2_{a_I}$ if family and within family selection methods are used.

In intra-population selection methods that use other populations as testers, genetic gain cannot be expressed in terms of the additive genetic variance of the base population except when gene frequencies in the two populations are equal. Topcrossing, which is actually half-sib testing, had been used primarily as a method of testing in recurrent selection for general combining ability and reciprocal recurrent selection methods. The latter selection procedure could also be done using full sibs, and as indicated in Table 2 expected genetic gain is similar for topcrossing and full-sib family selection except for differences in the components of phenotypic variance.

However, less labor and expense is involved for the same amount of selection differential if full sibs are used. If two-eared corn plants are selected for in reciprocal full-sib selection, higher and more stable yields could be expected in both populations and their hybrid combination (Lonnquist, 1967; Hallauer, 1968).

A logical consequence of the inbred-hybrid system of plant selection in corn is the search for a method that would improve the population performance and at the same time allow for an efficient extraction of superior hybrids.

Moll and Robinson (1966) compared intra-population full-sib selection to reciprocal recurrent selection with regards to their ability in improving the yield of corn varieties Jarvis and Indian Chief. They found reciprocal recurrent selection not as effective in improving the individual performance of the two varieties. They further concluded that full sib family testing is as effective as reciprocal recurrent

selection in the short term improvement of the variety cross. However, they had a higher selection differential in the full-sib test.

Kojima and Kelleher (1963), selecting for fecundity in *Drosophila pseudoobscura*, found reciprocal recurrent selection more effective than full-sib selection and realized progress in the crossbred progenies even if the purebreds do not respond to selection due to exhaustion of the additive genetic variance.

Lonnquist and Williams (1967) and Hallauer (1967) showed that extracting commercial hybrids using reciprocal full-sib selection was rapid, practical and productive. Combining this extraction method with reciprocal full-sib recurrent selection appears to offer tremendous promise as a practical breeding tool in corn improvement.

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THEORETICAL GAINS FOR DIFFERENT POPULATION

IMPROVEMENT PROCEDURES

Errata

Page 5, Line 4. The equation should be:

$$\sigma^2_{g_i} = \sum_{i=1}^{n} (p_i^2 a_i^2 + 2p_i q_i h_i^2 + q_i^2 a_i^2 - \bar{g}_1^2)$$

Page 7, line 23. Should be:

where $\bar{g}_3 = (p-q)a + pqh$ is the mean genotypic value of the S_1 progenies,

Page 11, line 23. Should be:

where $\hat{g}_5 = (pr-qs)a + [p+r(q-p)]h$ is the mean of the testcross

This equation could also be written:

$$\hat{g}_5 = (pr-qs)a + (ps+qr)h$$

which is a little simpler form.

Page 14. In Table 1, Col. 8, opposite genotype Bb, the h/a in two places should be h/2. It should be:

$$\left. \begin{array}{c} a/4 \\ h/2 \\ -a/4 \end{array} \right\} \quad h/2$$

The footnote for this column marked ¶ should read "Genotypic value of self progenies" instead of "Frequency of the favorable allele in self-progenies" which is given in Col. 4. Frequency in the self progeny is the same as in the parent.

Page 6, line 8. Perhaps it should be pointed out that if there is no correlation between genotype and environment, the regression of gene frequency on phenotypic value is the same as on genotypic value. Hence this equation could be written as

$$\Delta g_1 = \frac{S}{\sigma_P^2} \text{Cov } p_i g_i \frac{\delta \bar{g}_i}{\delta p_i} \qquad \text{for a single locus and as}$$

$$\Delta g = \frac{S}{\sigma_P^2} \sum_{i=1}^{n} \text{Cov } p_i g_i \frac{\delta g_i}{\delta p_i} \qquad \text{for all n loci.}$$

Therefore all following equations for Δg have σ_P^2 in the denominator.
Page 11, lines 1 and 5 and Table 2, p.17, Method A-7:
    Change the "fs" subscript on σ_P^2 and $\sigma_{P_{fs}}$ to "w", i.e. $\sigma_{P_w}^2$.
Bottom of page 15, add: $\sigma_{P_w}^2 = \sigma_w^2 + \sigma_n^{2fs} - \sigma_m^2$

$\sigma_{P_w}^2$ is the phenotypic variance among plants within half-sib families.