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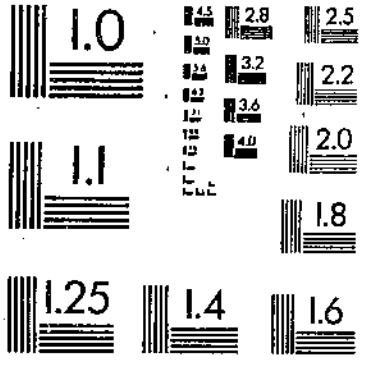

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Theoretical Improvement of Autotetraploid Crops: Interpopulation and Intrapopulation Selection

Abstract

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This paper presents equations for expected genetic progress for interpopulation and intrapopulation breeding schemes for autotetraploid crops. Equations are developed for the change in the genotypic means of a single population, a hybrid of two populations, and a synthetic variety of two populations with a single cycle of selection as a function of population parameters and change in allele frequency. Also, response equations are developed for changes in allele frequency and genotypic population means with intrapopulation breeding schemes, and more difficult response equations are developed for changes in genotypic mean of a hybrid population or synthetic variety as a function of breeding method.

KEYWORDS: autotetraploids, hybrid varieties, phenotypic selection, plant breeding, progeny testing, selection response, synthetic varieties.

Contents

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List of Tables

Theoretical Improvement of Autotetraploid Crops: Interpopulation and Intrapopulation Selection[1]

by D. E. Rowe and R. R. Hill, Jr.[2]

Introduction

The number of breeding alternatives that will attain a specific objective in a crop development program can be very large. To assist plant breeders in their decisionmaking processes of program development, the quantitative geneticists have developed some methodologies and mathematical models for theoretically comparing the expected gains of various breeding schemes under specific genetic situations. Those theoretical investigations can improve our understanding of published results and personal experiences in plant breeding. The theoretical investigations also provide a mechanism for making observations on and comparisons of breeding schemes in genetic situations which are neither possible or desirable in the field.

Theoretical research has been much more prolific for the diploid than for the autotetraploid organism, in part, because of the greater complexity of autotetraploid genetics. For instance, a population of diploid organisms not at random mating equilibrium will attain that equilibrium in two generations of random mating unlike the population of random mating autotetraploid organisms which approach random mating equilibrium only asymptotically. At a single locus with two or more different allelomorphs, the diploid has very few possible genotypes in comparison with the autotetraploid, and there is only one nonadditive genetic effect at a locus unlike the three for the autotetraploid. The diploid gamete of the autotetraploid also complicates the genetics of inheritance in comparison with that of the diploid with its haploid gamete.

In this publication, equations for expected genetic progress are presented for interpopulation and intrapopulation breeding schemes for autotetraploid crops. Previous publications (Haag *1973;* Hill *1971;* Hill and Byers *1979;* Hill and Haag *1974;* Rowe *1980;* Rowe and Hill *1981*),[3] present some of the results that are reported here in consistent notation and in detail generally not possible in journal articles.

In chapter 1, equations are developed for the change in the genotypic means of a single population, a hybrid of two populations, and a synthetic variety of two populations with a single cycle of selection as a function of population parameters and change in allele frequency. Because each expression is derived two ways, there is some repetition.

In chapter 2, response equations are developed for changes in allele frequency and genotypic population mean with intrapopulation breeding schemes.

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[3]The year in italic, when it follows the author's name, refers to List of References, p. 31.

Chapter 3 combines results of chapters 1 and 2 for development of the more difficult response equations for changes in genotypic mean of a hybrid population or synthetic variety as a function of breeding method.

For those who have difficulty understanding the sometimes complex algebra or the basic methodology in this publication, we suggest a review of the bulletin by Empig et al. *1972*. Calculations for a given breeding situation are much less protracted in diploid genetics than in autotetraploid genetics.

1. Population Models

Introduction

For theoretical investigations of autotetraploid genetics, simplifying assumptions of the genetic situation keeps the often protracted mathematical calculations from being absolutely insolvable. For our purposes, we investigate the genetics at a single locus with only two alleles (*B* and *b*). The simplifying assumptions are (1) all populations are initially at random mating equilibrium (RME) with respect to the locus of interest, (2) only random chromosomal segregation occurs, and (3) allele frequencies are unaffected by any factor other than selection. Other simplifying assumptions appear in the text as needed.

For the modeling, there are three base populations (*P*, *R*, and *U*). The frequencies of alleles *B* and *b* are, respectively, p and q in population *P*, r and s in population *R*, and u and v in population *U*. The expected frequencies of the five possible genotypes with RME are given for each base population in table 1. The array of frequencies for each base population is a binomial expansion to the fourth power of $(p+q)$, $(r+s)$, or $(u+v)$.

Table 1.—Notation for genotypic frequencies in each base population at random mating equilibrium

Genotypes	Base populations		
	P	*R*	*U*
BBBB	p^4	r^4	u^4
BBBb	$4p^3q$	$4r^3s$	$4u^3v$
BBbb	$6p^2q^2$	$6r^2s^2$	$6u^2v^2$
Bbbb	$4pq^3$	$4rs^3$	$4uv^3$
bbbb	q^4	s^4	v^4

The mathematical model used to describe the genetic effects in the five genotypes of population *P*, the equations for the four population parameters (α, β, γ, and δ), and the genetic variances, appear in table 2 (Hill *1971*). The *R* population model and equations for population parameters are found by substituting r and s, respectively, for p and q of table 2; similarly for the U population model, u and v are substituted, respectively, for the p and q of table 2.

The expressions for genotypic values (table 2) of the autotetraploid model (Hill *1971*) are determined with reference only to the *B* allele. Terms *A*, *D*, *T*, and *F* are, respectively, the genetic effects of the individual allele (*B*), the interaction of two alleles (*BB*), the interaction of three alleles (*BBB*), and the interaction of four alleles (*BBBB*) at a locus. The coefficients for each of those terms indicate the different ways a specific effect can be generated from a genotype and can be found by use of combinatorial analysis. For instance, the coefficient for the *D* component of the triplex genotype (*BBBb*) is found as the number of ways a grouping of two *B* alleles can occur in a group of three *B* alleles, that is symbolically C^3_2, which is 3.

Table 2.—The mathematical model of genotypic values of genotypes in population *P* and the equations for population parameters and their variances (Hill 1971)

Genotypes	Genotypic value[1]
BBBB	$4A + 6D + 4T + F$
BBBb	$3A + 3D + T$
BBbb	$2A + D$
Bbbb	A
bbbb	0

Genetic effects	Genotypic variances[2]
Additive $(\alpha) = A + 3pD + 3p^2T + p^3F$	Additive variance $(\sigma^2_A) = 4pq\alpha^2$
Digenic $(\beta) = D + 2pT + p^2F$	Digenic variance $(\sigma^2_D) = 6p^2q^2\beta^2$
Trigenic $(\gamma) = T + pF$	Trigenic variance $(\sigma^2_T) = 4p^3q^3\gamma^2$
Quadrigenic $(\delta) = F$	Quadrigenic variance $(\sigma^2_F) = p^4q^4\delta^2$

[1]The *A*, *D*, *T*, and *F* are genetic effects associated with individual alleles, and the interaction of 2, 3, and 4 alleles, respectively.
[2]The total genetic variance (σ^2_G) is $\sigma^2_A + \sigma^2_D + \sigma^2_T + \sigma^2_F$.

With five genotypes, the genetic effect at a single locus of the theoretical population can be described completely by four parameters, additive (α), digenic (β), trigenic (γ), and quadrigenic (δ) (table 2). The additive and digenic parameters of the autotetraploid population have interpretations that are analogous to the additive and dominance parameters of the diploid population. The trigenic and quadrigenic parameters have no diploid counterparts.

The equations for genetic parameters and their variances (table 2) were found by the procedure of successive differences that was outlined in detail by Li (*1957*).

The equations for genotypic values (table 2) differ from the autotetraploid genetic models of Kempthorne (*1957*) and Li (*1957*). The Hill (*1971*) model is a one-to-one transformation of the other two-allele models and, from our experience, has superior characteristics for algebraic manipulations.

Allele Frequency and Change With Selection

The intent of selection is to improve the genotypic mean of a population by increasing the frequency of the desirable allele(s) in a population. With a single cycle of selection, the expected change in frequency of one allele, say *B*, is approximated by the following relationship (Falconer *1960*, chapter 11).

$$dp = \frac{S\sigma_{xy}}{\sigma^2_{Ph}}. \qquad (1)$$

The dp denotes the changes in frequency of allele B. The S is the selection differential expressed as phenotypic standard deviations of the parental generation, and σ^2_{Ph} is the phenotypic variance. The covariance (σ_{xy}) relates the frequency of allele B in the selected units (x) to the genotypic values of the observed units (y) upon which the selections are based.

Change in Genotypic Mean of Population With Selection

The mean genotypic value of a population is given by $\Sigma f_i G_i (i = 1, \ldots, 5)$ where f_i is the frequency of the i^{th} genotype and G_i is the mean genotypic value of the i^{th} genotype. For population P at RME, the frequency of the i^{th} genotype appears in table 1 under P, and the genotypic value of the i^{th} genotype appears in table 2 under Genotypic Value. The mean genotypic value ($\overline{P}$) of population P at RME is

$$\overline{P} = 4pA + 6p^2D + 4p^3T + p^4F. \tag{2}$$

With a single cycle of selection, the frequency of allele B will change by a quantity dp, and the mean of the improved population ($\overline{P}'$) at RME is

$$\overline{P}' = 4(p + dp)A + 6(p + dp)^2D + 4(p + dp)^3T + (p + dp)^4F \tag{3}$$

The change in mean genotypic value ($\triangle\overline{P}$) of the population is the difference between the old and new means $(\overline{P}' - \overline{P}) = \triangle\overline{P}$, thus

$$\begin{aligned}\triangle\overline{P} = {} & 4dpA + (12pdp + 6dp^2)D + (12p^2dp + 12pdp^2 + 4dp^3)T \\ & + (4p^3dp + 6p^2dp^2 + 4pdp^3 + dp^4)F.\end{aligned} \tag{4}$$

(Throughout this text in each term of an equation, the allele frequency, such as p, always precedes the term for change in frequency, such as dp.)

A single cycle of selection usually results in a small change in allele frequency, and the square and greater powers of the change are considered negligible and are ignored to simplify the equations. Thus equation (4) can be simplified.

$$\triangle\overline{P} = 4dpA + 12pdpD + 12p^2dpT + 4p^3dpF. \tag{5}$$

First the terms of this equation are arranged.

$$\begin{aligned}&\triangle\overline{P} = dp(4A + 12pD + 12p^2T + 4p^3F). \quad \text{Then} \\ &\triangle\overline{P} = 4dp\alpha_{(P)}\end{aligned} \tag{6}$$

where $\alpha_{(P)}$ is the additive genetic effect of population P (table 2). In equation (6), the change in population mean with one generation of selection is a function of the additive genetic effect and dp.

The change in the population mean can also be found by use of a calculus method described by Moreno-Gonzalez and Grossman (*1976*) for a diploid population. This method expresses the changes in mean $\triangle\overline{P}$ with a change in p as a Taylor expansion of derivatives to the fourth degree. The Taylor expansion for the change in the mean is

$$\triangle P = \frac{\Theta P}{\Theta p}dp + \frac{\Theta^2 P}{\Theta p^2}(dp)^2 + \frac{\Theta^3 P}{\Theta p^3}(dp)^3 + \frac{\Theta^4 P}{\Theta p^4}(dp)^4$$

where $\Theta P/\Theta p$, . . . $\Theta^4 P/\Theta p^4$ are partial derivatives of the first to fourth degrees, respectively, of P with respect to p.

The solutions for these partial derivatives are as follows:

$$\frac{\Theta P}{\Theta p} = 4A + 12pD + 12p^2T + 4p^3F = 4\alpha$$

$$\frac{\Theta^2 P}{\Theta p^2} = 12D + 24pT + 12p^2F = 12\beta$$

$$\frac{\Theta^3 P}{\Theta p^3} = 24T + 24pF = 24\gamma$$

$$\frac{\Theta^4 P}{\Theta p^4} = 24F = 24\delta.$$

Therefore, $\triangle\overline{P} = 4\alpha dp + 12\beta dp^2 + 24\gamma dp^3 + 24\delta dp^4$.

If squares and higher powers of dp are ignored as before, $\triangle\overline{P}$ is again $4dp\alpha_{(P)}$. Computationally, the use of the Taylor expansion facilitates analytical solutions in terms of population parameters. The difficulty in the computations with the direct subtraction method will become apparent shortly.

Unpublished results indicate that the use of the approximate equation for $\triangle\overline{P}$, equation (5), instead of the exact equation, equation (4), has some error.[4] For certain types of inheritance, the frequency p where $\triangle\overline{P}$ was maximized differed by 7 percentage points for the two methods, but generally the difference was very slight. Usually, equation (5) overestimated $\triangle\overline{P}$ slightly, but in one case it overestimated the maximum $\triangle\overline{P}$ by 24 percent. Further research may indicate that the error introduced by use of an approximate equation for $\triangle\overline{P}$ is intolerable.

Change in Genotypic Mean of a Population Hybrid With Selection

The genotypic mean of a hybrid of two populations P and R (hereafter called the hybrid mean) is found easily by recalling that P has three types of gametes (*BB, Bb,* and *bb*), which occur at frequencies of p^2, $2pq$, and q^2, respectively, in population P at RME. In population R, the same gametes occur, respectively, at frequencies of r^2, $2rs$, and s^2. Construction of a Punnett square with those arrays of gametes and frequencies in the margins of adjacent sides will, when multiplied in all combinations, give the genotypic products and their frequencies in a hybrid (see table 3). The hybrid mean is then $\Sigma f_i G_i$, where f_i is frequency of each genotype (table 3) and G_i is the mean genotypic value of the respective genotypes (table 2). After simplification, the hybrid mean ($\overline{X}_{Hyb}$) of $P \times R$ is

$$\overline{X}_{Hyb} = (2p + 2r)A + (p^2 + 4pr + r^2)D + (2p^2r + 2pr^2)T + p^2r^2F. \qquad (7)$$

[4]Rowe, D. E. 1980. Calculated inherent error in presently used equations for intrapopulation improvement procedures. [Unpublished.]

Table 3.—Punnett square for calculating frequencies of genotypes in a hybrid of population *P* and *R*

		Population *R* Gametes/(frequency)		
		BB (r^2)	*Bb* ($2rs$)	*bb* (s^2)
Population *P* Gametes/(frequency)	*BB* (p^2)	*BBBB* (p^2r^2)	*BBBb* ($p^2 2rs$)	*BBbb* (p^2s^2)
	Bb ($2pq$)	*BBBb* ($2pqr^2$)	*BBbb* ($4pqrs$)	*Bbbb* ($2pqs^2$)
	bb (q^2)	*BBbb* (q^2r^2)	*Bbbb* ($q^2 2rs$)	*bbbb* (q^2s^2)

The change in the hybrid mean due to changes in allele frequencies in the parent populations is found in a manner analogous to that described previously for selection within a single population. Let dp be the change in allele frequency in population P and dr be the change in allele frequency in population R. The new hybrid mean ($\overline{X}'_{Hyb}$) is

$$\overline{X}'_{Hyb} = [2(p+dp) + 2(r+dr)]A + [(p+dp)^2 + 4(p+dp)(r+dr) + (r+dr)^2]D + [2(p+dp)(r+dr)^2 + 2(p+dp)^2(r+dr)]T + (p+dp)^2(r+dr)^2F. \quad (8)$$

The change in the hybrid mean ($\triangle\overline{X}_{Hyb}$) is found by subtraction,

$$\triangle\overline{X}_{Hyb} = \overline{X}'_{Hyb} - \overline{X}_{Hyb}$$
$$\triangle\overline{X}_{Hyb} \simeq [2dp + 2dr]A + [2pdp + dp^2 + 4rdp + 4pdr + 4dpdr + 2rdr + dr^2]D + [2p^2dr + 4prdp + 4pdpdr + 2rdp^2 + 2dp^2dr + 4prdr + 2pdr^2 + 2r^2dp + 4rdpdr + 2dpdr^2]T + [2p^2rdr + p^2dr^2 + 2pr^2dp + 4prdpdr + 2pdpdr^2 + r^2dp^2 + 2rdp^2dr + dp^2dr^2]F.$$

If the quadratic and bilinear terms involving dp and dr are considered negligible and ignored, this equation simplifies to

$$\triangle\overline{X}_{Hyb} = 2dp(A + 3rD + 3r^2T + r^3F) + 2dr(A + 3pD + 3p^2T + p^3F) + 2dp(p-r)(D + 2rT + r^2F) - 2dr(p-r)(D + 2pT + p^2F). \quad (9)$$

Substitution of population parameters into equation (9) gives

$$\triangle\overline{X}_{Hyb} = 2dp\alpha_{(R)} + 2dr\alpha_{(P)} + (p-r)(2dp\beta_{(R)} - 2dr\beta_{(P)}). \quad (10)$$

The expression for change in the hybrid mean can be found by use of the methodology of Moreno-Gonzalez and Grossman (*1976*). The general expression for the change in the mean of a population affected by two parameters p and r as a Taylor expansion to the fourth degree is

$$d\bar{X} = (\Theta X/\Theta p)dp + (\Theta X/\Theta r)dr + (\Theta^2 X/\Theta p^2)dp^2/2 + (\Theta^2 X/\Theta r^2)dr^2/2 + 2(\Theta^2 X/\Theta p \Theta r)(dpdr)/2 + (\Theta^3 X/\Theta p^3)dp^3/6 + 3(\Theta^3 X/\Theta p^2 \Theta r)(dp^2 dr)/6 + 3(\Theta^3 X/\Theta p \Theta r^2)(dpdr^2)/6 + (\Theta^3 X/\Theta r^3)dr^3/6 + (\Theta^4 X/\Theta p^4)dp^4/24 + 4(\Theta^4 X/\Theta p^3 \Theta r)dp^3 dr/24 + 6(\Theta^4 X/\Theta p^2 \Theta r^2)(dr^2 dp^2)/24 + 4(\Theta^4 X/\Theta p \Theta r^3)dpdr^3/24 + (\Theta^4 X/\Theta r^4)dr^4/24. \quad (11)$$

The partial derivatives are solved (see table 4) and substituted into equation (11). In terms of population parameters, the change in the hybrid mean is

$$\Delta\bar{X}_{Hyb} = [2\alpha_{(R)} + 2(p-r)\beta_{(R)}]dp + [2\alpha_{(P)} - 2(p-r)\beta_{(P)}]dr + \beta_{(R)}dp^2 + [2\beta_{(P)} + 2\beta_{(R)} + 2(p-r)^2\delta]dpdr + \beta_{(P)}dr^2 + 2\gamma_{(R)}dp^2 dr + 2\gamma_{(P)}dpdr^2 + \delta dp^2 dr^2. \quad (12)$$

When the bilinear, quadratic, and higher powers of dp and dr are ignored, equation (12) will simplify to equation (10).

Table 4.—Solutions for partial derivatives used in the calculations of change in genotypic mean of a hybrid of populations *P* and *R* as a Taylor expansion to the fourth degree

Derivative[1]	Solutions
$(\theta X/\theta p)$	$= 2A + 2pD + 4rD + 4prT + 2r^2T + 2pr^2F = 2\alpha_{(R)} + 2(p-r)\beta_{(R)}$
$(\theta X/\theta r)$	$= 2A + 4pD + 2rD + 2p^2T + 4prT + 2p^2rF = 2\alpha_{(P)} - 2(p-r)\beta_{(P)}$
$(\theta^2 X/\theta p^2)$	$= 2D + 4rT + 2r^2F = 2\beta_{(R)}$
$(\theta^2 X/\theta r^2)$	$= 2D + 4pT + 2p^2F = 2\beta_{(P)}$
$(\theta^2 X/\theta p \theta r)$	$= 4D + 4pT + 4rT + 4prF = 2\beta_{(P)} + 2\beta_{(R)} - 2(p-r)^2\delta$
$(\theta^3 X/\theta p^3)$	$= 0$
$(\theta^3 X/\theta p^2 \theta r)$	$= 4T + 4rF = 4\gamma_{(R)}$
$(\theta^3 X/\theta p \theta r^2)$	$= 4T + 4pF = 4\gamma_{(P)}$
$(\theta^3 X/\theta r^3)$	$= 0$
$(\theta^4 X/\theta p^2 \theta r^2)$	$= 4F = 4\delta$
$(\theta^4 X/\theta p^4)$	$= (\theta^4 X/\theta p^3 \theta r) = (\theta^4 X/\theta p \theta r^3) = \theta^4 X/\theta r^4) = 0$

[1] $\bar{X}_{Hyb} = (2p + 2r)A + (p^2 + 4pr + r^2)D + (2p^2 r + 2pr^2)T + p^2 r^2 F$.

Change in Genotypic Mean of Synthetic Variety With Selection

For theoretical purposes, the synthetic variety of interest is derived with quantitatively equal contributions of genetic material from two populations, *P* and *R*. The frequency of allele *B* in the synthetic variety will be $(p + r)/2$. When this 2-population synthetic variety attains RME, the genotypic mean is given by equation (2) with $(p + r)/2$ substituted for p. When expanded, this equation for the genotypic mean of the synthetic variety (hereafter called synthetic mean) is

$$\bar{X}_{Syn} = [2p + 2r]A + [3/2)p^2 + 3pr + (3/2)r^2]D + [(1/2)p^3 + (3/2)p^2r + (3/2)pr^2 + (1/2)r^3]T + [(1/16)p^4 + (4/16)p^3r + (6/16)p^2r^2 + (4/16)pr^3 + (1/16)r^4]F. \quad (13)$$

As before, let dp be the change in allele frequency with selection in population P and dr be the change in allele frequency with selection in population R. The synthetic mean following selection is found by substituting $(p + dp)$ and $(r + dr)$ for p and r, respectively, in equation (13).

$$\begin{aligned}\bar{X}'_{Syn} = {} & [(2p + 2dp) + (2r + 2dr)]A + [(3/2)(p^2 + 2pdp + dp^2) \\ & + 3(pr + pdr + rdp + dpdr) \\ & + (3/2)(r^2 + 2rdr + dr^2)]D + [(1/2)(p^3 + 3p^2dp + 3pdp^2 + dp^3) \\ & + (3/2)(p^2r + p^2dr + 2prdp + rdp^2 + 2pdpdr + dp^2dr) \\ & + (3/2)(pr^2 + pdr^2 + 2prdr + r^2dp + 2rdpdr + dr^2dp) \\ & + (1/2)(r^3 + 3r^2dr + 3rdr^2 + dr^3)]T \\ & + [(1/16)(p^4 + 4p^3dp + 6p^2dp^2 + 4pdp^3 + dp^4) \\ & + (4/16)(p^3r + p^3dr + 3p^2dpdr + 3prdp^2 + 3p^2rdp + 3pdp^2dr + rdp^3 + dp^3dr) \\ & + (6/16)(p^2r^2 + 2p^2rdr + p^2dr^2 + 2pr^2dp + 4prdpdr \\ & + 2pdpdr^2 + r^2dp^2 + 2rdp^2dr + dp^2dr^2) \\ & + (4/16)(pr^3 + 3pr^2dr + 3prdr^2 + pdr^3 + r^3dp + 3r^2dpdr + 3rdpdr^2 + dpdr^3) \\ & + (1/16)(r^4 + 4r^3dr + 6r^2dr^2 + 4rdr^3 + dr^4)]F. \end{aligned} \quad (14)$$

If the bilinear, quadratic, and higher order terms are assumed to be negligible, then equation (14) simplifies to

$$\begin{aligned}\bar{X}'_{Syn} = {} & [(2p + 2dp) + (2r + 2dr)]A \\ & + [(3/2)(p^2 + 2pdp) + 3(pr + pdr + rdp) + (3/2)(r^2 + 2rdr)]D \\ & + [(1/2)(p^3 + 3p^2dp) + (3/2)(p^2r + p^2dr + 2prdp) + (3/2)(pr^2 \\ & + 2prdr + r^2dp) + (1/2)(r^3 + 3r^2dr)]T + [(1/16)(p^4 + 4p^3dp) \\ & + (4/16)(p^3r + p^3dr + 3p^2rdp) + (6/16)(p^2r^2 + 2p^2rdr + 2pr^2dp) \\ & + (4/16)(pr^3 + 3pr^2dr + r^3dp) + (1/16)(r^4 + 4r^3dr)]F. \end{aligned}$$

The change in the synthetic mean after selection is found by subtraction

$$\begin{aligned}(\bar{X}'_{Syn} - \bar{X}_{Syn}) &= \Delta\bar{X}_{Syn} \\ \Delta\bar{X}_{Syn} &= 2dpA + 3pdpD + 3rdpD + 2drA + 3pdrD + 3rdrD + (3/2)p^2dpT + 3prdpT \\ &\quad + (3/2)r^2dpT + (3/2)p^2drT + 3prdrT + (3/2)r^2drT + (1/4)p^3dpF \\ &\quad + (3/4)p^2rdpF + (3/4)pr^2dpF + (1/4)r^3dpF + (1/4)p^3drF + (3/4)p^2rdrF \\ &\quad + (3/4)pr^2drF + (1/4)r^3drF. \end{aligned} \quad (15)$$

Equation (15) can be expressed in terms of population parameters:

$$\begin{aligned}\Delta\bar{X}_{Syn} = {} & 2dp\alpha_{(R)} + 2dr\alpha_{(P)} + (9/4)(p - r)(dp\beta_{(R)} - dr\beta_{(P)}) \\ & + (3/4)(p - r)(dp\beta_{(P)} - dr\beta_{(R)}) + (1/2)(p - r)^3(dp\delta - dr\delta). \end{aligned} \quad (16)$$

The change in the synthetic mean via selection in the parental populations can be found by use of the Taylor expansion. The general formula for the Taylor expansion is equation (11), and the solutions to the partial derivatives are found in table 5. Substitution of the partial derivatives into equation (11) gives the change in the synthetic mean.

$$\Delta\overline{X}_{Syn} = [\alpha_{(P)} + \alpha_{(R)} - ((3/4)(p-r)^2(\gamma_{(P)} + \gamma_{(R)}))](dp + dr)$$
$$+ [(3/2)\beta_{(P)} + (3/2)\beta_{(R)} - ((3/4)(p-r)^2\delta)](1/2)(dp + dr)^2$$
$$+ [(3/2)\gamma_{(P)} + (3/2)\gamma_{(R)}](1/6)(dp + dr)^3 + [(3/2)\delta(1/24)](dp + dr)^4.$$

Ignoring quadratic and higher order terms of dp and dr, the $\Delta\overline{X}_{Syn}$ is

$$\Delta\overline{X}_{Syn} = (dp + dr)[\alpha_{(P)} + \alpha_{(R)} - ((3/4)(p-r)^2(\gamma_{(P)} + \gamma_{(R)}))]. \quad (17)$$

With considerable algebraic manipulation, equation (16) can be shown to be equivalent to equation (17).

The difference in the expected change in the genotypic mean of the synthetic variety (17) and the hybrid (10) is the effect of the disequilibrium of genotype frequencies found in the hybrid.

Table 5.—Solutions for partial derivatives used in the calculations of change with selection in the genotypic mean of the 2-population synthetic variety as a Taylor expansion to the fourth degree

Derivative[1]	Solutions
$(\theta X/\theta p)$	$= 2A + 3pD + 3rD + (3/2)p^2T + 3prT + (3/2)r^2T + (1/4)p^3F$
	$+ (3/4)p^2rF + (3/4)pr^2F + (1/4)r^3F$
	$= \alpha_{(P)} + \alpha_{(R)} - (3/4)(p-r)^2(\gamma_{(P)} + \gamma_{(R)})$
$(\theta X/\theta r)$	$= 2A + 3pD + 3rD + (3/2)p^2T + 3prT + (3/2)r^2T + (1/4)p^3F$
	$+ (3/4)p^2rF + (3/4)pr^2F + (1/4)r^3F$
	$= \alpha_{(P)} + \alpha_{(R)} - (3/4)(p-r)^2(\gamma_{(P)} + \gamma_{(R)})$
$(\theta^2X/\theta p^2)$	$= 3D + 3pT + 3rT + (3/4)p^2F + (3/2)prF + (3/4)r^2F$
	$= (3/2)\beta_{(P)} + (3/2)\beta_{(R)} - (3/4)(p-r)^2\delta$
$(\theta^2X/\theta p^2)$	$= (\theta^2X/\theta p\theta r) = (\theta^2X/\theta r^2)$
$(\theta^3X/\theta p^3)$	$= 3T + (3/2)pF + (3/2)rF = (3/2)(\gamma_{(P)} + \gamma_{(R)})$
$(\theta^3X/\theta p^3)$	$= (\theta^3X/\theta p^2\theta r) = (\theta^3X/\theta p\theta r^2) = (\theta^3X/\theta r^3)$
$(\theta^4X/\theta p^4)$	$= (3/2)F = (3/2)\delta$
$(\theta^4X/\theta p^4)$	$= (\theta^4X/\theta p^3\theta r) = (\theta^4X/\theta p^2\theta r^2) = (\theta^4X/\theta p\theta r^3) = (\theta^4X/\theta r^4)$

[1] $\overline{X} = (2p + 2r)A + ((3/2)p^2 + (3/2)r^2)D + ((1/2)p^3 + (3/2)p^2r + (3/2)pr^2 + (1/2)r^3)T$
$+ ((1/16)p^4 + (4/16)p^3r + (6/16)p^2r^2 + (4/16)pr^3 + (1/16)r^4)F.$

Summary

Equations (6), (10), and (17) indicate that changes in the genotypic means, respectively, of the single population, hybrid, and synthetic variety are determined by change or changes in allele frequency and the additive genetic component or components. When p and r are not equal, the digenic and trigenic components in equations (10) and (17), respectively, could significantly influence the change in the genotypic mean. Without knowing the mode of genetic action at the B locus the positive or negative contribution of the nonadditive genetic effects to the change in the genotypic mean is not predictable. As p and r approach equality, the nonadditive effects in equations (10) and (17) go to zero and $\Delta\overline{X}_{Hyb} = \Delta\overline{X}_{Syn}$ because $\alpha_{(P)} = \alpha_{(R)}$.

2. Intrapopulation Improvement

Introduction

Selection schemes are classified as either intra- or interpopulation improvement methods. The delimiting factor of this classification is the final objective of the breeding method. An intrapopulation breeding method is for improving the mean genotypic value of a single population while an interpopulation breeding method is for improving the mean genotypic value of a hybrid or synthetic variety.

With a single cycle of selection, the change in mean genotypic value of a population can be expressed as a function of change in allele frequency. The algorithm is to find a solution for equation (1) which corresponds to a particular breeding method and substitute it into the equation for change in mean genotypic value, equation (6). The two important components of equation (1) are the covariance (σ_{xy}) and the ratio of selection differential to phenotypic variance (S/σ^2_{Ph}). In this chapter, the influence of breeding method on σ_{xy} is demonstrated with S/σ^2_{Ph} assigned the constant value of *"k"*. In the summary of this chapter, the influence of breeding method on S/σ^2_{Ph} is discussed.

The covariances associated with each breeding method are presented in a manner that shows their derivation, but the calculation of the covariance is sometimes much simplified by the use of two identities. The covariance is unaffected by subtraction of a constant from one of the variables, and the multiplication of one of the variables by a constant multiplies the covariances by the same constant.

The theoretical response to selection is in terms of gain for a single cycle of selection. Since the number of generations of a crop necessary for a cycle of selection depends upon the breeding method, meaningful comparisons of breeding methods should be on the basis of a gain per generation or some fixed period of time, but even this is only approximate. Other factors which may unequally affect generation time of breeding schemes are the breeding objectives and the procedures and facilities of the plant breeder.

Genetic Advance With Intrapopulation Selection Schemes

Mass Selection 1 (Mass 1)

With this breeding scheme (also known as simple recurrent selection (Allard *1960*) and phenotypic recurrent selection (Penny et al. *1963*)), individual plants of a population are selected on the basis of their phenotype and then randomly mated to generate the seed for a new, select population. To simplify the mathematics, we assume that the selected population, in this case and all subsequent cases of intrapopulation selection, has attained RME.

The covariance (σ_{xy}) of equation (1) is found for mass 1 and all other breeding schemes as $\Sigma f_i g_i p_i - \overline{gp}$ where f_i is the frequency of the i^{th} genotype, g_i is the genotypic value of the observed unit corresponding to the i^{th} genotype, and p_i is the frequency of the desired allele in the selected unit of i^{th} genotype. The $\overline{g}$ is the mean genotypic value of the observed units, and $\overline{p}$ is the mean frequency of allele *B* in units from which selections are made.

Thus, for mass 1 selection, the genotype is in column 1 of table 6, the frequency of genotype (f_i) in column 2, the frequency of the allele B (p_i) in the respective genotypes in column 3, and the respective genotypic value in column 4. The mean frequency of allele B among the units from which selections are made, that is, the individual plants, is p and the mean genotypic value among the observed units, the same plants, is the mean genotypic value of the population given by equation (2). Thus, this covariance is between the genotypic value and frequency of allele B in the individual. The covariance for mass 1 selection is

$$\begin{aligned}\sigma_{xy_{\text{mass 1}}} &= p^4(1)(4A + 6D + 4T + F) + 4p^3q(3/4)(3A + 3D + T) + 6p^2q^2(1/2)(2A + D) \\ &\quad + 4pq^3(1/4)A + q^4(0)(0) - p(4pA + 6p^2D + 4p^3T + p^4F) \\ &= A(4p^4 + 9p^3 - 9p^4 + 6p^2 - 12p^3 + 6p^4 + p - 3p^2 + 3p^3 - p^4 - 4p^2) \\ &\quad + D(6p^4 + 9p^3 - 9p^4 + 3p^2 - 6p^3 + 3p^4 - 6p^3) + T(4p^4 + 3p^3 - 3p^4 - 4p^4) \\ &\quad + F(p^4 - p^5).\end{aligned}$$

This simplifies to

$$\begin{aligned}\sigma_{xy_{\text{mass 1}}} &= (p - p^2)A + (3p^2 - 3p^3)D + (3p^3 - 3p^4)T + (p^4 - p^5)F \\ &= pqA + 3p^2qD + 3p^3qT + p^4qF.\end{aligned}$$

The change in allele frequency expressed in terms of population parameter is

$$dp = kpq\alpha_{(P)} \tag{18}$$

where subscript (P) indicates "of population P" and k is the constant $Si\sigma^2_{Ph}$. The change in the genotypic mean of population P with one cycle of selection with mass 1 selection is, from equation (6),

$$\Delta\overline{P}_{\text{mass 1}} = 4kpq\alpha^2_{(P)}. \tag{19}$$

Thus, the change in population mean with this selection is a function of the allele frequency and the square of the additive population parameter or k times the additive genetic variance.

Mass Selection 2 (Mass 2)

With this scheme, individual plants are selected on the basis of their phenotype, but seed is produced from selections which were polycrossed to the entire population of selected and unselected plants. The genotypic values of the phenotypes are in column 4 of table 6, genotypes of the polycross progenies are in column 7, and their respective frequencies are in column 8. The frequencies of allele B in polycross progenies of selected plants are in column 10, whose entries are the products of columns 8 and 9. The mean frequency of B in column 10 is p, and the mean genotypic value of column 4 is given by equation (2). The covariance of mass 2 selection is the corrected sum of cross products of columns 2, 4, and 10 of table 6.

$$\begin{aligned}\sigma_{xy_{\text{mass 2}}} &= (p^4)((p + 1)/2)(4A + 6D + 4T + F) + (p^3q)(2p + (3/2))(3A + 3D + T) \\ &\quad + (p^2q^2)(3p + (3/2))(2A + D) + (pq^3)(2p + (1/2))A + (q^4)(0)(p/2) \\ &\quad - p(4pA + 6p^2D + 4p^3T + p^4F).\end{aligned}$$

Table 6.—The progenies, frequencies, and genotypic values for calculation of covariances for breeding methods involving phenotypic selection or polycross progenies

Individual plant characteristics						Progeny from polycrossing					
Genotype	Genotype frequency	Frequency of '*B*'	Genotypic value	Gametes	Gamete frequency	Polycross genotypes	Genotype frequency	Frequency of '*B*'	Mean frequency of '*B*'	Mean genotypic value	Frequency of '*B*' in next polycross
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
BBBB	p^4	1	$4A + 6D + 4T + F$	*BB*	1	*BBBB*	p^2	1	$(1/2) + (p/2)$	$2(p + 1)A + (1 + 4p + p^2)D + (2p^2 + 2p)T + p^2F$	$1/4 + (3/4)p$
						BBBb	$2pq$	3/4			
						BBbb	q^2	1/2			
BBBb	$4p^3q$	3/4	$3A + 3D + T$	*BB*	1/2	*BBBB*	$p^2/2$	1	$(3/8) + (p/2)$	$(2p + (3/2))A + (p^2 + 3p + (1/2))D + ((3/2)p^2 + p)T + (p^2/2)F$	$3/16 + (3/4)p$
				Bb	1/2	*BBBb*	pq	3/4			
						BBbb	$q^2/2$	1/2			
						BBBb	$p^2/2$	3/4			
						BBbb	pq	1/2			
						Bbbb	$q^2/2$	1/4			
BBbb	$6p^2q^2$	1/2	$2A + D$	*BB*	1/6	*BBBB*	$p^2/6$	1	$(1/4) + (p/2)$	$(2p + 1)A + (p^2 + (1/6))D + (p^2 + (p/3))T + (p^2/6)F$	$1/8 + (3/4)p$
				Bb	4/6	*BBBb*	$2pq/6$	3/4			
				bb	1/6	*BBbb*	$q^2/6$	1/2			
						BBBb	$4p^2/6$	3/4			
						BBbb	$8pq/6$	1/2			
						Bbbb	$4q^2/6$	1/4			
						BBbb	$p^2/6$	1/2			
						Bbbb	$2pq/6$	1/4			
						bbbb	$q^2/6$	0			
Bbbb	$4pq^3$	1/4	A	*Bb*	1/2	*BBBb*	$p^2/2$	3/4	$(1/8 + (p/2)$	$(2p + (1/2))A + (p^2 + p)D + (p^2/2)T$	$1/16 + (3/4)p$
				bb	1/2	*BBbb*	$2pq/2$	1/2			
						Bbbb	$q^2/2$	1/4			
						BBbb	$p^2/2$	1/2			
						Bbbb	$2pq/2$	1/4			
						bbbb	$q^2/2$	0			
bbbb	q^4	0	0	*bb*	1	*BBbb*	p^2	1/2	$p/2$	$2pA + p^2D$	$(3/4)p$
						Bbbb	$2pq$	1/4			
						bbbb	q^2	0			

This covariance is greatly simplified by subtracting ($p/2$) from the entries of column 10, which are then one-half of column 3, and the covariance for mass 2 is one-half of that of mass 1. Thus,

$$\sigma_{xy_{\text{mass 2}}} = (pq\alpha)/2, \tag{20}$$

and the corresponding change in population mean is

$$\Delta\overline{P}_{\text{mass 2}} = 2kpq\alpha^2_{(P)}. \tag{21}$$

The polycross pollination of selected individuals prior to selection halves the expected change per cycle of selection.

Mass Selection 3 (Mass 3)

In this breeding scheme, individual plants are selected on the basis of their individual phenotype following self-pollination. The selfed progeny of the selected individuals are then randomly intermated to generate the select population. With selfing, the allele frequencies of the progeny are expected to be the same as those of the parent. Thus, this selection scheme has the covariance of mass 1, but the generation time is doubled.

S1 Progeny Test (S1PT)

With this breeding scheme, individual plants are selected on the basis of the performance of their selfed progenies. The selected individuals are then randomly crossed to generate a select population. Information for calculations of covariance is in columns 2 and 3 of table 6, which were used previously, and in column 7 of table 7. The mean genotypic value of each progeny from selfing is found by noting that the gametes of each genotype, column 3, occur at frequencies in column 4, which produce the genotypes in column 5 with the frequencies in column 6. The mean genotypic value for each parental genotype is found by multiplying the genotypic value associated with each genotype of column 5 by its frequency, column 6. The frequency of allele B in all units of selection is p and the mean genotypic value ($\overline{g}$) is determined by multiplying the genotypic values of the genotypes in column 5 by their respective frequencies in column 6 and the seed parent frequency, column 2. The mean is

$$\overline{g} = 4pA + p(5p + 1)D + 2p^2(2p + 1)T + (p^3 + \frac{p^2q^2}{6})F.$$

The covariance is

$$\begin{aligned}\sigma_{xy_{(S1PT)}} &= (p^4)(1)(4A + 6D + 4T + F) + 4p^3q(3/4)[3A + (13/4)D + (3/2)T + (1/4)F] \\ &\quad + 6p^2q^2(1/2)[2A + (4/3)D + (1/3)T + (1/36)F] + 4pq^3(1/4)[A + (1/4)D] \\ &\quad + q^4(0)(0) - p[4pA + p(5p + 1)D + 2p^2(2p + 1)T + (p^2/6)(p^2 + 4p + 1)F] \\ &= pq[A + (3p + (1 - 2p)/4)D + (3p^2 - (3p^2 - 2p)/2)T \\ &\quad + (p^3 + (-10p^3 + 6p^2 + p)/12)F] \\ &= pq\alpha_{(P)} + pq[((1 - 2p)/4)D - ((3p^2 - 2p)/2)T - ((10p^3 - 6p^2 - p)/12)F]. \end{aligned} \tag{22}$$

Table 7.—Products, frequencies, and genotypic values with selfing of population *P*

Seed parent		Gametes with selfing		Progeny with selfing		
Genotype	Frequency	Genotype	Frequency	Genotype	Frequency	Mean genotypic value
(1)	(2)	(3)	(4)	(5)	(6)	(7)
BBBB	p^4	*BB*	1	*BBBB*	1	$4A + 6D + 4T + F$
BBBb	$4p^3q$	*BB*	1/2	*BBBB*	1/4	$3A + (13/4)D + (3/2)T + (1/4)F$
		Bb	1/2	*BBBb*	2/4	
				BBbb	1/4	
BBbb	$6p^2q^2$	*BB*	1/6	*BBBB*	1/36	$2A + (4/3)D + (1/3)T + (1/36)F$
		Bb	4/6	*BBBb*	2/9	
		bb	1/6	*BBbb*	1/2	
				Bbbb	2/9	
				bbbb	1/36	
Bbbb	$4pq^3$	*BB*	1/2	*BBbb*	1/4	$A + (1/4)D$
		Bb	1/2	*Bbbb*	1/2	
				bbbb	1/4	
bbbb	q^4	*bb*	1	*bbbb*	1	0

Thus, the covariance of S1PT is a function of allele frequency, genetic parameter $\alpha_{(P)}$, and some portion of nonadditive genetic effects (D, T, and F). The change in genotypic mean with selection is

$$\Delta\overline{P}_{S1PT} = 4kpq\alpha_{(P)}(\alpha_{(P)} + C) \qquad (23)$$

where C is $[((1-2p)/4)D + ((3p^2-2p)/2)T - ((10p^3-6p^2-p)/12)F]$.
Since C is dependent upon the values of p, D, T, and F, it is not obvious when C is positive or negative.

A slight variant of the S1PT is the selection of best S1 families instead of the parental clone. Since the mean allele frequency of selfed progeny is the same as that of the parent, the covariance is not changed.

Half-sib Progeny Test (HSPT)

With this breeding scheme, also known as polycross progeny test (Tysdal and Kiesselbach *1944*), individual plants are selected on the basis of their half-sib family performance. The half-sib families are produced by polycrossing or pollinating the flowers of each plant with pollen that is representative of the entire population. The selections are then randomly crossed to produce the

select population. The information necessary for covariance calculation is found in columns 2, 3, and 11 of table 6. The mean genotypic values for the half-sib families is found by multiplying the respective genotypic values of the genotypes of column 7 by the frequency of the genotype, column 8. The mean frequency of allele B in all the parental plants is p, and the mean genotypic value of progeny with random mating is that of the population mean given by equation 2. The covariance is

$$\begin{aligned}\sigma_{xy_{(HSPT)}} = {} & p^4(1)[(2p+2)A + (p^2+4p+1)D + (2p^2+2p)T + p^2F] + 4p^3q(3/4)[(2p+(3/2))A \\ & + (p^2+3p+(1/2))D + ((3/2)p^2+p)T + ((1/2)p^2)F] \\ & + 6p^2q^2(1/2)[(2p+1)A + (p^2+2p+(1/6))D + (p^2+(p/3))T + ((1/6)p^2)F] \\ & + 4pq^3(1/4)[(2p+(1/2))A + (p^2+p)D + ((1/2)p^2)T] + q(0)(2pA + p^2D) \\ & - p[4pA + 6p^2D + 4p^3T + p^4F] \\ \sigma_{xy_{(HSPT)}} = {} & (pq/2)(A + 3pD + 3p^2T + p^3F) = (pq/2)\alpha_{(P)}. \end{aligned} \tag{24}$$

Thus, the change in the genotypic mean of a population with a single cycle of selection is

$$\triangle\overline{P}_{(HSPT)} = 2kpq\alpha^2_{(P)}. \tag{25}$$

Half-sib Family Selection (HSFS)

With this procedure, half-sib families are generated and evaluated as in the previous breeding scheme, but the half-sib families are selected instead of the parent plant. These families are intercrossed to produce the select population. Columns 2, 10, and 11 of table 6 contain information for calculation of the covariance. The mean frequency of allele B in all half-sib families is p, and the mean genotype value of these progenies is given by equation (2). The covariance is

$$\begin{aligned}\alpha_{xy_{(HSFS)}} = {} & p^4((1+p)/2)[2(p+1)A + (1+4p+p^2)D + (2p^2+2p)T + p^2F] \\ & + 4p^3q[(3/8)+(p/2)][(2p+(3/2))A + (p^2+3p+(1/2))D \\ & + ((3/2)p^2+p)T + (p^2/2)F] + 6p^2q^2((1/4))+(p/2))[(2p+1)A \\ & + (p^2+2p+(1/6))D + (p^2+(p/3))T + (p^2/6)F] \\ & + 4pq^3[(1/8)+(p/2)]\,[(2p+(1/2))A + (p^2+p)D + (p^2/2)T] \\ & + q^4(p/2)(2pA + p^2D) - p[4pA + 6p^2D + 4p^3T + p^4F]. \end{aligned}$$

This covariance is simplified by subtracting $(p/2)$ from column 10 of table 6 to get values that are one-half of those in column 3. Then, the covariance of HSFS is one-half of the covariance of HSPT. Thus,

$$\sigma_{xy_{(HSFS)}} = (pq/4)\alpha_{(P)}, \tag{26}$$

and the change in the genotypic mean is

$$\triangle\overline{P}_{(HSFS)} = kpq\alpha^2_{(P)}. \tag{27}$$

Half-sib Progeny Test With Family Progeny Selection (HSFP)

This breeding scheme is identical to HSFS selection just described, except all families are polycrossed and the seed of superior families are collected. The progenies of the selected families are intercrossed to produce the select population. Columns 2, 11, and 12 of table 6 contain the information for covariance calculation. The allele frequencies in the progeny of polycrossed half-sib families, column 12, were generated in the same manner as frequencies of column 10. The mean genotypic value of the random mating population is that of the single population (equation (2)), and the frequency of *B* in progeny of the half-sib families is *p*. The covariance for HSFP is

$$\begin{aligned}\sigma_{xy_{(HSFP)}} = {} & p^4[(1/4)+(3/4)p][2(p+1)A+(1+4p+p^2)D+(2p^2+2p)T+p^2F] \\ & + 4p^3q[(3/16)+(3/4)p][(2p+(3/2))A+(p^2+3p+(1/2))D \\ & + ((3/2)p^2+p)T+(p^2/2)F]+6p^2q^2[(1/8)+(3/4)p][(2p+1)A \\ & + (p^2+2p+(1/6))D+(p^2+(p/3))T+(p^2/6)F] \\ & + 4pq^3[(1/16)+(3/4)p][2p+(1/2))A+(p^2+p)D+(p^2/2)T] \\ & + q^4[(3/4)p][2pA+p^2D]-p[4pA+6p^2D+4p^3T+p^4F].\end{aligned}$$

This covariance is greatly simplified by subtraction of $(3p/4)$ from each entry in column 12 of table 6 to get values that are one-fourth of those in column 3. Thus, this covariance is one-fourth of the covariance of HSPT. Thus,

$$\sigma_{sy_{(HSFP)}} = (pq/8)\alpha_{(P)}, \tag{28}$$

and the change in the genotypic mean of the population with a single cycle of selection is

$$\Delta\overline{P}_{(HSFP)} = (kpq/2)\alpha^2_{(P)}. \tag{29}$$

Full-sib Family Selection (FSF)

With this breeding scheme, full-sib families are generated by the crossing of randomly selected pairs of plants from a population of individuals. The best full-sib families are selected and randomly crossed to generate the select population. The covariance is calculated with the information in columns 2, 3, and 4 of table 8. With five genotypes, there are 25 possible full-sib combinations, but some of those are reciprocals of each other. Thus, there are only 15 different full-sib pairings, and they appear in column 1 of table 8. The frequency of allele *B* over all the randomly generated families is that of the parent population, *p*. The mean genotypic value of these families is the same as that of the parent population. The covariance is

$$\begin{aligned}\sigma_{xy_{(FSF)}} = {} & p^8(1)[4A+6D+4T+F]+(8p^7q)(7/8)[7/2)A+(9/2)D+(5/2)T \\ & + (1/2)F]+12p^6q^2(3/4)[3A+(19/6)D+(4/3)T+(1/6)F]+8p^5q^3(5/8)[5/2)A \\ & + 2D+(1/2)T]+2p^4q^4(1/2)[2A+D]+16p^6q^2(3/4)[3A+(13/4)D+(3/2)T \\ & + (1/4)F]+48p^5q^3(5/8)[(5/2)A+(13/6)D+(3/4)T+(1/12)F] \\ & + 32p^4q^4(1/2)[2A+(5/4)D+(1/4)T]+8p^3q^5(3/8)[(3/2)A+(1/2)D] \\ & + 36p^4q^4(1/2)[2A+(4/3)D+(1/3)T+(1/36)F]+48p^3q^5(3/8)[(3/2)A \end{aligned}$$ (cont.)

$$+ (2/3)D + (1/12)T] + 12p^2q^6(1/4)[A + (1/6)D] + 16p^2q^6(1/4)[A + (1/4)D]$$
$$+ 8pq^7(1/8)[(1/2)A] - p[4pA + 6p^2D + 4p^3T + p^4F].$$

This lengthy equation simplifies to

$$(\sigma_{xy_{(FSF)}} = (pq/2)\alpha_{(p)}, \tag{30}$$

and the expected change in genotypic mean

$$\Delta\overline{P}_{(FSF)} = 2kpq\alpha^2_{(p)}. \tag{31}$$

A slight variant of full-sib family selection is the selection of the parental clones instead of their families. The expected gain is the same because the mean allele frequency of full-sib families is the same as the mean allele frequency of the two parental clones.

Table 8.—The frequencies and genotypic values for calculation of covariance with full-sib family selection

Full-sib family matings	Frequency of matings	Frequency of *B* in matings	Mean genotypic value of full-sib families
(1)	(2)	(3)	(4)
BBBB × *BBBB*	p^8	1	$4A + 6D + 4T + F$
BBBB × *BBBb*	$8p^7q$	7/8	$(7/2)A + (9/2)D + (5/2)T + (1/2)F$
BBBB × *BBbb*	$12p^6q^2$	3/4	$3A + (19/6)D + (4/3)T + (1/6)F$
BBBB × *BBbb*	$8p^5q^3$	5/8	$(5/2)A + 2D + (1/2)T$
BBBB × *bbbb*	$2p^4q^4$	1/2	$2A + D$
BBBb × *BBBb*	$16p^6q^2$	3/4	$3A + (13/4)D + (3/2)T + (1/4)F$
BBBb × *BBbb*	$48p^5q^3$	5/8	$(5/2)A + (13/6)D + (3/4)T + (1/12)F$
BBBb × *Bbbb*	$32p^4q^4$	1/2	$2A + (5/4)D + (1/4)T$
BBBb × *bbbb*	$8p^3q^5$	3/8	$(3/2)A + (1/2)D$
BBbb × *BBbb*	$36p^4q^4$	1/2	$2A + (4/3)D + (1/3)T + (1/36)F$
BBbb × *Bbbb*	$48p^3q^5$	3/8	$(3/2)A + (2/3)D + (1/12)T$
BBbb × *bbbb*	$12p^2q^6$	1/4	$A + (1/6)D$
Bbbb × *Bbbb*	$16p^2q^6$	1/4	$A + (1/4)D$
Bbbb × *bbbb*	$8pq^7$	1/8	$(1/2)A$
bbbb × *bbbb*	q^8	0	0

Modified Ear-to-Row (MER)

This breeding scheme is a two-stage breeding method that combined half-sib family selection and phenotypic selection of individual plants (Webel and Lonquist *1967*). In the first stage, half-sib families are produced for each plant by pollinating each with pollen that is genetically representative of the entire population. The best half-sib families are selected, and then the best plants are selected on the basis of their individual phenotypes. All selections are then randomly intercrossed to produce the new, select population.

With this breeding procedure, selection occurs twice, and the allele frequency is changed twice. The first stage of this procedure is half-sib family selection (HSFS), and that covariance was determined earlier as $\sigma_{xy_{(HSFS)}} = (pq/4)\alpha_{(p)}$. The covariance of the second stage is between the genotypic value and the frequency of allele *B* of the individuals within the half-sib families. Thus, the covariance is calculated for each of the five possible genotypes of the seed parent (column 1 of table 6), and the covariance for stage 2 of selection is the weighted average of those five covariances.

The information for calculation of the second-stage covariance for MER is in table 6. The genotype of the seed parent of each half-sib family is in column 1. The genotype and frequencies of the half-sib families are in columns 7 and 8, respectively. The frequency of allele *B* in each genotype is in column 9. The mean frequency of allele *B* within a half-sib family is found by multiplying the entries of column 8 by those of column 9; those means are in column 10. The mean genotypic value of a half-sib family is found by an analogous method. For each genotype in column 7, the frequency of the genotype, column 8, is multiplied by its respective genotypic value (table 2), and the sum of those products is the mean genotypic value of each half-sib family, column 11 of table 6. The frequencies of the half-sib families are in column 2.

The second stage covariance (σ_{xy})

$$\begin{aligned}\sigma'_{xy} = {} & p^4[p^2(1)(4A + 6D + 4T + F) + 2pq(3/4)(3A + 3D + T) + q^2(1/2)(2A + D) \\ & - ((1/2) + (p/2))(2(p + 1)A + (1 + 4p + p^2)D + (2p^2 + 2p)T + p^2F)] \\ & + 4p^3q[(p^2/2)(1)(4A + 6D + 4T + F) + ((p + pq)/2)((3/4)(3A + 3D + T) \\ & + ((pq + q)/2)(1/2)(2A + D) + (q^2/2)(1/4)(A) - ((3/8) + (p/2)) \\ & ((2p + (3/2))A + (p^2 + 3p + (1/2))D + ((3/2)p^2 + p)T + (p^2/2)F)] \\ & + 6p^2q^2[(p^2/6)(1)(4A + 6D + 4T + F) + ((p + p^2)/3)(3/4)(3A + 3D + T) \\ & + ((1/6) + pq)(1/2)(2A + D) + ((q^2 + q)/3)(1/4)A - ((1 + 2p)/4)((2p + 1)A \\ & + (p^2 + 2p + (1/6))D + (p^2 + (p/3))T + (p^2/6)F] \\ & + 4pq^3[(p^2/2)(3/4)(3A + 3D + T) + ((pq + p)/2)(1/2)(2A + D) \\ & + ((pq + q)/2)(1/4)(A) + (q^2/2)(0)(0) - ((1/8) + (p/2))((2p + (1/2))A \\ & + (p^2 + p)D + (p^2/2)T)] + q^4[p^2(1/2)(2A + D) + 2pq(1/4)A + q^2(0)(0) \\ & - (p/2)(2pA + p^2D)].\end{aligned}$$

The covariance for stage 2 simplifies to

$$\sigma'_{xy} = (3/4)pq\alpha_{(P)}, \tag{32}$$

and the change in the genotypic mean with MER is

$$\begin{aligned}\Delta\overline{P}_{MER} &= 4\alpha_{(P)}(k(1/4)pq\alpha_{(P)} + k'(3/4)pq\alpha_{(P)}) \\ &= kpq\alpha^2_{(P)} + 3k'pq\alpha^2_{(P)}.\end{aligned} \tag{33}$$

The prime on the second *k* indicates that this *k* value is not expected to be identical to the first *k*.

An alternative procedure for MER selection is to save seed from the best plants within selected families in the evaluation nursery. If those plants had

been randomly intercrossed with all plants of the nursery instead of just the selections, the frequencies of B alleles would be one-half of those in column 9 of table 6 plus $(p/2)$. With subtraction of $(p/2)$, the covariance of the second stage of selection is $\alpha_{xy} = (3/8)pq\alpha_{(P)}$, and the change in the genotypic mean at stage 2 would be half of that with selection prior to pollination.

Topcross Progeny Test (TX)

With this breeding scheme, the individuals of population P are pollinated with a representative sample of pollen from a different population (U), designated the tester population. The best parents are selected on basis of performance of topcross progeny. These selected parents are randomly intercrossed to produce the select population. The covariance is determined with the information in columns 2, 3, and 5 of table 9. The genotypic mean of topcross progenies, column 5, is found in a manner analogous to that used for the genotypic mean of polycrossed families, column 11 of table 6. In population U, the ratio of gametes ($BB : Bb : bb$) is $u^2 : 2uv : v^2$, respectively. Thus, u and v are substituted for p and q, respectively, in column 11 of table 6 to give means in column 5 of table 9. The frequency of allele B among plants of population P is p, and the mean genotypic value of the topcross progenies is the hybrid of two populations (from equation (7)) which is $(2p + 2u)A + (p^2 + 4pu + u^2)D + (2p^2u + 2pu^2)T + p^2u^2F$. The covariance for the topcross progeny is

$$\begin{aligned}\sigma_{xy_{(TX)}} = {} & p^4(1)[(2 + 2u)A + (1 + 4u + u^2)D + (2u + 2u^2)T + u^2F] + 4p^3q(3/4) \\ & [((3/2) + 2u)A + ((1/2) + 3u + u^2)D + ((u + (3/2)u^2)T + (1/2)u^2F] \\ & + 6p^2q^2(1/2)[(1 + 2u)A + ((1/6) + 2u + u^2)D + ((1/3)u + u^2)T + (1/6)u^2F] \\ & + 4pq^3(1/4)[((1/2) + 2u)A + (u + u^2)D + (1/2)u^2T] + q^4(0)[2uA + u^2D] \\ & - p[(2p + 2u)A + (p^2 + 4pu + u^2)D + (2p^2u + 2pu^2)T + p^2u^2F].\end{aligned}$$

Table 9.—Means, allele frequencies, and genotypic values for calculation of covariances for topcross selection schemes

Seed parent			Polycrossed seed parent (frequency of allele B)	Genotypic mean of topcross progeny
Genotype	Genotype frequency	Frequency of allele B		
(1)	(2)	(3)	(4)	(5)
$BBBB$	p^4	1	$(1/2) + (p/2)$	$(2 + 2u)A + (1 + 4u + u^2)D + (2u + 2u^2)T + u^2F$
$BBBb$	$4p^3q$	3/4	$(3/8) + (p/2)$	$((3/2 + 2u)A + ((1/2) + 3u + u^2)D + (u + (3/2)u^2)T + (1/2)u^2F$
$BBbb$	$6p^2q^2$	1/2	$(1/4) + (p/2)$	$(1 + 2u)A + ((1/6) + 2u + u^2)D + ((1/3)u + u^2)T + (1/6)u^2F$
$Bbbb$	$4pq^3$	1/4	$(1/8) + (p/2)$	$((1/2) + 2u)A + (u + u^2)D + (1/2)u^2T$
$bbbb$	q^4	0	$(p/2)$	$2uA + u^2D$

The covariance simplifies to

$$\sigma_{xy_{(TX)}} = (1/2)pq(\alpha_{(U)} + (p - u)\beta_{(U)}), \tag{34}$$

and the change in the genotypic mean is

$$\Delta\overline{P}_{(TX)} = 2kpq\alpha_{(P)}(\alpha_{(U)} + (p - u)\beta_{(U)}). \tag{35}$$

Thus, the change in the genotypic mean of population P is a function of additive effects in both populations, digenic effects in the tester population, and the difference in allele frequencies of the two populations.

Topcross Progeny Test With Polycross Progeny (TXPX)

With this breeding scheme, the topcross progenies are produced as before, but simultaneously the plants of tested populations are polycrossed. The best clones are determined as before, but their respective progenies from polycrossing are randomly crossed to produce the select population. The information for the covariance calculation is in columns 2, 4, and 5 of table 9. The frequency of B in the polycross families is p, and the mean genotypic value of topcross progenies is that of the hybrid. The covariance for this procedure is

$$\begin{aligned}\sigma_{xy\,(TXPX)} = {} & p^4((1/2) + (p/2))[(2 + 2u)A + (1 + 4u + u^2)D + (2u + 2u^2)T + u^2F] \\ & + 4p^3q((3/8) + (p/2))[((3/2) + 2u)A + ((1/2) + 3u + u^2)D + (u + (3/2)u^2)T \\ & + (1/2)u^2F] + 6p^2q^2((1/4) + (p/2))[(1 + 2u)A + ((1/6) + 2u + u^2)D \\ & + ((1/3)u + u^2)T + (1/6)u^2F] + 4pq^3((1/8) + (p/2))[((1/2) + 2u)A \\ & + (u + u^2)D + (1/2)u^2T] + q^4(p/2)[2uA + u^2D] - p[(2p + 2u)A \\ & + (p^2 + 4pu + u^2)D + (2p^2u + 2pu^2)T + p^2u^2F].\end{aligned}$$

This covariance is simplified by subtraction of $p/2$ from entries of column 4 of table 9 to get values one-half of those in column 3. Therefore, this covariance is one-half of covariance for TX and

$$\sigma_{xy_{(TXPX)}} = (pq/4)(\alpha_{(U)} + (p - u)\beta_{(U)}). \tag{36}$$

The change in the genotypic mean is

$$\Delta\overline{P}_{(TXPX)} = kpq\alpha_{(P)}(\alpha_{(U)} + (p - u)\beta_{(U)}). \tag{37}$$

Topcross Progeny Test With Full-sib Progeny (TXFS)

This breeding scheme is an alternative to selection of polycrossed families in TXPX. With this scheme, random full-sib pairings are made in the population which is to be improved while test crosses are made simultaneously as in TX and TXPX procedures. The seed from best full-sib families is selected on basis of performance of average of respective topcross progenies. The information necessary for the covariance calculation is in columns 2, 3, and 4 of table 10. The frequency of B in all full-sib families is the same as that of the base population, p, and the mean genotypic value of all topcross families is that of the hybrid, equation (7). The covariance is

$$\sigma_{xy_{(TXFS)}} = p^8(1)[(2+2u)A + (1+4u+u^2)D + (2u+2u^2)T + u^2F]$$
$$+ 8p^7q(7/8)[((7/4)+2u)A + ((3/4)+(7/2)u+u^2)D + ((3/4)u$$
$$+ (7/4)u^2)T + (3/4)u^2F] + 12p^6q^2(3/4)[((3/2)+2u)A + ((7/12)$$
$$+ 3u+u^2)D + ((7/6)u + (3/2)u^2)T + (7/12)u^2F] + 8p^5q^3(5/8)[((5/4)$$
$$+ 2u)A + ((1/2)+(5/2)u+u^2)D + (u+(5/4)u^2)T + (1/2)u^2F]$$
$$+ 2p^4q^4(1/2)[(1+2u)A + ((1/2)+2u+u^2)D + (u+u^2)T + (1/2)u^2F]$$
$$+ 16p^6q^2(3/4)[((3/2)+2u)A + ((1/2)+3u+u^2)D + (u+(3/2)u^2)T$$
$$+ (1/2)u^2F] + 48p^5q^3(5/8)[((5/4)+2u)A + ((1/3)+(5/2)u+u^2)D$$
$$+ ((2/3)u+(5/4)u^2)T + (1/3)u^2F] + 32p^4q^4(1/2)[(1+2u)A$$
$$+ ((1/4)+2u+u^2)D + ((1/2)u+u^2)T + (1/4)u^2F] + 8p^3q^5(3/8)[((3/4)+2u)A$$
$$+ ((1/4)+(3/2)u+u^2)D + ((1/2)u+(3/4)u^2)T + (1/4)u^2F]$$
$$+ 36p^4q^4(1/2)[(1+2u)A + ((1/6)+2u+u^2)D + ((1/3)u+u^2)T + (1/6)u^2F]$$
$$+ 48p^3q^5(3/8)[((3/4)+2u)A + ((1/12)+(3/2)u+u^2)D + ((1/6)u$$
$$+ (3/4)u^2)T + (1/12)u^2F] + 12p^2q^6(1/4)[((1/2)+2u)A + ((1/12)$$
$$+ u+u^2)D + ((1/6)u + (1/2)u^2)T + (1/12)u^2F] + 16p^2q^6(1/4)[((1/2)$$
$$+ 2u)A + (u+u^2)D + (1/2)u^2T] + 8pq^7(1/8)[((1/4)+2u)A + ((1/2)u+u^2)D$$
$$+ (1/4)u^2T] + q^8(0)(2uA + u^2D) - p[(2p+2u)A + (p^2+4pu+u^2)D$$
$$+ (2p^2u+2pu^2)T + p^2u^2F].$$

After much simplification, this covariance becomes

$$\sigma_{xy_{(TXFS)}} = (pq/4)(\alpha_{(U)} + (p-u)\beta_{(U)}), \tag{38}$$

which is the same as the covariance for TXPX and therefore

$$\triangle\overline{P}_{(TXFS)} = \triangle\overline{P}_{(TXPX)} = kpq\alpha_{(P)}(\alpha_{(U)} + (p-u)\beta_{(U)}. \tag{39}$$

Table 10.—Matings, frequencies, and genotypic values for calculation of covariance for topcrossing with selection of full-sib families

Full-sib family matings	Frequency of matings	Frequency of *B* in matings	Mean genotypic value of topcross families
(1)	(2)	(3)	(4)
BBBB × *BBBB*	p^8	1	$(2+2u)A + (1+4u+u^2)D + (2u+2u^2)T + u^2F$
BBBB × *BBBb*	$8p^7q$	7/8	$((7/4)+2u)A + ((3/4)+(7/2)u+u^2)D + ((3/2)u+(7/4)u^2)T + (3/4)u^2F$
BBBB × *BBbb*	$12p^6q^2$	3/4	$((3/2)+2u)A + ((7/12)+3u+u^2)D + ((7/3)u+(3/2)u^2)T + (7/12)u^2F$
BBBB × *Bbbb*	$8p^5q^3$	5/8	$((5/4)+2u)A + ((1/2)+(5/2)u+u^2)D + (u+(5/4)u^2)T + (1/2)u^2F$
BBBB × *bbbb*	$2p^4q^4$	1/2	$(1+2u)A + ((1/2)+2u+u^2)D + (u+u^2)T + (1/2)u^2F$
BBBb × *BBBb*	$16p^6q^2$	3/4	$((3/2)+2u)A + ((1/2)+3u+u^2)D + (u+(3/2))u^2)T + (1/2)u^2F$
BBBb × *BBbb*	$48p^5q^3$	5/8	$((5/4)+2u)A + ((1/3)+(5/2)u+u^2)D + ((2/3)u+(5/4)u^2)T + (1/3)u^2F$
BBBb × *Bbbb*	$32p^4q^4$	1/2	$(1+2u)A + ((1/4)+2u+u^2)D + ((1/2)u+u^2)T + (1/4)u^2F$
BBBb × *bbbb*	$8p^3q^5$	3/8	$((3/4)+2u)A + ((1/4)+(3/2)u+u^2)D + ((1/2)u+(3/4)u^2)T + (1/4)u^2F$
BBbb × *BBbb*	$36p^4q^4$	1/2	$(1+2u)A + ((1/6)+2u+u^2)D + ((1/3)u+u^2)T + (1/6)u^2F$
BBbb × *Bbbb*	$48p^3q^5$	3/8	$((3/4)+2u)A + ((1/12)+(3/2)u+u^2)D + ((1/6)u+(3/4)u^2)T + (1/12)u^2F$
BBbb × *bbbb*	$12p^2q^6$	1/4	$((1/2)+2u)A + ((1/12)+u+u^2)D + ((1/6)u+((1/2)u^2)T + (1/12)u^2F$
Bbbb × *Bbbb*	$16p^2q^6$	1/4	$((1/2)+2u)A + (u+u^2)D + (1/2)u^2T$
Bbbb × *bbbb*	$8pq^7$	1/8	$((1/4)+2u)A + ((1/2)u+u^2)D + (1/4)u^2T$
bbbb × *bbbb*	q^8	0	$2uA + u^2D$

Summary

Any comparison of the relative effectiveness of breeding schemes discussed in this chapter should involve the component S/σ^2_{Ph} of equation (1) which was assigned the arbitrary value k for the derivation of $\Delta\overline{P}$'s. The response equation for selection indicated that the desirable properties of a breeding method are (1) a large coefficient for the covariance as derived in this chapter and (2) a minimal phenotypic variance (σ^2_{Ph}). From table 11, it is apparent that the components of σ^2_{Ph} are not constant for all breeding schemes. To some extent, the environmental component of σ^2_{Ph} can be reduced by refinement of screening methods and choice of experimental design as well as choice of breeding method.

Table 11.—The theoretical expected changes of 12 intrapopulation breeding schemes and their phenotypic variances

Method	Expected change ($\Delta\overline{P}$) in population P mean	Generations per selection cycle	Phenotypic variance[1] (σ^2_{Ph})
Mass (1)	$4kpq\alpha^2_{(P)}$	1	$\sigma^2_w + \sigma^2_G$
Mass (2)	$2kpq\alpha^2_{(P)}$	2	$\sigma^2_w + \sigma^2_G$
Mass (3)	$4kpq\alpha^2_{(P)}$	2	$\sigma^2_w + \sigma^2_G$
S1PT	$4kpq\alpha_{(P)}(\alpha_{(P)} + {}^2C)$	3	$(\sigma^2_w + \sigma^2_{S1} - \sigma^2_{S1F})/rn + \sigma^2_e/r + \sigma^2_{S1F}$
HSPT	$2kpq\alpha^2_{(P)}$	2 or 3	$(\sigma^2_w + \sigma^2_G - \sigma^2_{HS})/rn + \sigma^2_e/r + \sigma^2_{HS}$
HSFS	$kpq\alpha^2_{(P)}$	2 or 3	$(\sigma^2_w + \sigma^2_G - \sigma^2_{HS})/rn + \sigma^2_e/r + \sigma^2_{HS}$
HSFP	$(1/2)kpq\alpha^2_{(P)}$	3 or 4	$(\sigma^2_w + \sigma^2_G - \sigma^2_{HS})/rn + \sigma^2_e/r + \sigma^2_{HS}$
FSF	$2kpq\alpha^2_{(P)}$	2 or 3	$(\sigma^2_w + \sigma^2_G - \sigma^2_{FS})/rn + \sigma^2_e/r + \sigma^2_{FS}$
MER stage 1	$kpq\alpha^2_{(P)}$		
MER stage 2	$3k'pq\alpha^2_{(P)}$	2	$(\sigma^2_w + \sigma^2_G - \sigma^2_{HS})/n + \sigma^2_e$
TX	$2kpq\alpha_{(P)}(\alpha_{(U)} + (p-u)\beta_{(U)})$	3	$(\sigma^2_w + \sigma^2_{GTX} - \sigma^2_{TX})/rn + \sigma^2_e/r + \sigma^2_{TX}$
TXPX	$kpq\alpha_{(P)}(\alpha_{(U)} + (p-u)\beta_{(U)})$	3	$(\sigma^2_w + \sigma^2_{GTX} - \sigma^2_{TX})/rn + \sigma^2_e/r + \sigma^2_{TX}$
TXFS	$kpq\alpha_{(P)}(\alpha_{(U)} + (p-u)\beta_{(U)})$	3	$(\sigma^2_w + \sigma^2_{GTX} - \sigma^2_{TX})/rn + \sigma^2_e/r + \sigma^2_{TX}$

[1] σ^2_w, σ^2_G, σ^2_{S1}, σ^2_{S1F}, σ^2_{HS}, σ^2_e, σ^2_{FS}, σ^2_{GTX}, σ^2_{TX}, r, and n are, respectively, variance, total genetic variance, total genetic variance in an S1 population, variance due to S1 family means, variance due to half-sib family means, error variance, variance due to full-sib family means, total genetic variance of a set of topcross families, variance due to topcross family means, replications of a progeny, and number of plants in a progeny plot.

[2] $C = ((1-2p)/4)D - ((3p^2-2p)/2)T - ((10p^3-6p^2-p)/12)F$.

The selection of "best" breeding method in theory is altered in reality by the trait for selection, reproductive characteristics of the crop, and limits of the breeder's labor, expertise, facilities, and funds. To facilitate a critique of the investigated breeding methods, a specific reference crop is needed, in this case, alfalfa (*Medicago sativa* L.). Briefly, alfalfa is a perennial that requires approximately 4 months from seeding to flowering in the greenhouse, can be

cloned easily with stem cuttings, does not reliably produce seed with selfing, produces an abundance of flowers on mature plants, and can be clipped back severely and brought into flowering several times during a summer. It is commonly field-planted in drilled rows or broadcast, but may be space planted for breeding purposes.

The information summarized in table 11 can be used to predict the effectiveness of some breeding schemes for alfalfa. The three versions of mass selection have a large covariance, property 1. The covariance of mass 2 is half of that of mass 1 and mass 3 but still greater than that of most other methods (table 11). Mass 1 is the most attractive of the mass-selection methods, since isolation and pollination of selected plants would not normally be a problem with alfalfa. Mass 3 is impractical for alfalfa because it requires the production of selfed seed. Mass 2 would be recommended over mass 1 only if the isolation and crossing of selected individuals took more than twice the time of seed production without isolation. These mass-selection methods do not have property 2, the minimal phenotypic variance, and may be ineffective for improvement of some traits because of the large environmental influence in the variance.

The S1PT procedure provides good control of the phenotypic variance and has a large coefficient for the covariance. Direct comparison of the covariance of S1PT with covariances of other methods is frustrated by component "C" (table 11). Unpublished results by Rowe[5] indicate that the covariance S1PT is smaller than that of mass 1 when "*B*" exhibits monoplex dominance to "*b*"; but with less complete dominance the covariances become equal, and with duplex dominance S1PT is superior. With additive gene action, the covariances are identical. The S1PT procedure is probably of little value for alfalfa breeding because of the requirement for selfed seed.

The HSPT procedure provides good control of phenotypic variation and has a relatively large covariance. Neither the production of half-sib seed nor the saving of parental plants until evaluation of the progenies presents a serious problem with alfalfa. The cost in labor, facilities, and time for progeny testing will limit the number of plants that can be evaluated in a given period of time. Hill et al. (*1971*) concluded that if HSPT were to be more effective than mass 1, the heritability of a trait would have to be very low.

The HSFS procedure also has good control over phenotypic variance, but the covariance is one-half of that for HSPT (table 11). HSFS does not require saving the parent plants until progenies are evaluated. Saving the parent alfalfa plants is not usually a problem, so the HSFS procedure would definitely be inferior to HSPT.

[5]Rowe, D. E. 1980. Theoretical investigation of the expected gains with selfed progeny test selection (S1PT) and phenotypic selection (mass(1)). [Unpublished.]

The FSF procedure has good control of phenotypic variance, and the covariance equals that for HSPT. Unlike HSPT, FSF does not require saving the parents for progeny evaluation, but is expected to require more labor to produce the full-sib seed. The random pairings could increase bias in the progeny evaluation, since the random pairing of good and poor plants would produce inferior progenies.

The MER procedure is a combination of HSFS and mass 1 procedures. With alfalfa, the full-sib families could be evaluated in replicated fields, and the second stage selections could be made in a space-planted nursery. The same trait does not have to be selected at both stages. Hill and Byers (*1979*) concluded that MER selection would have to operate on a large scale to be more effective than mass 1.

The covariances for the topcross selection procedures are not analytically comparable to the procedures just discussed because of the terms involving the tester population. The singular comparison was a study by Rowe and Hill (*1981*) which concluded the TX procedure would be superior to HSPT for any traits determined by a gene with monoplex dominance, if the frequency of the desirable allele were lower in the tester population than in the selected population.

3. Interpopulation Improvement

Introduction

In this chapter, we describe our investigation of the two simplest objectives possible for interpopulation improvement, improvement of the mean genotypic values of the two-population hybrid and the two-population synthetic variety. The construction of response equations for change in the mean genotypic value of either the hybrid or synthetic variety proceeds as outlined for the intrapopulated improvement procedures in chapter 2. Briefly, an expression is developed by use of equation (1) for the change of allele frequency with selection in two populations, *P* and *R*. Those expressions for *dp* and *dr* are substituted into equations (10) or (17) to predict the change in the genotypic mean of the hybrid or synthetic variety, respectively. Equations (10) and (17) are reproduced below for reference

$$\Delta\overline{X}_{HYB} = 2dp\alpha_{(R)} + 2dr\alpha_{(P)} + (p - r)(2dp\beta_{(R)} - 2dr\beta_{(P)}). \quad (10)$$

$$\Delta\overline{X}_{Syn} = (dp + dr)[\alpha_{(P)} + \alpha_{(R)} - ((3/4)(p - r)^2(\gamma_{(P)} + \gamma_{(R)}))]. \quad (17)$$

Theoretical expressions are developed for the change in the means of the two-population hybrid and two-population synthetic variety with a single cycle of selection with various interpopulation breeding methods. The equations of different breeding methods are compared directly where possible. Other comparisons which require assumptions of modes of genic action are also described.

Select and Combine Procedures (SC)

With this breeding method, each of the base populations, *P* and *R*, is improved by use of a single cycle of selection with any intrapopulation improvement method, except the topcross, described in chapter 2. The same or different intrapopulation breeding methods may be used on the two base populations. The two improved populations, *P'* and *R'*, are the parents of the improved hybrid or synthetic variety.

For example, if a cycle of mass 1 selection is used in both *P* and *R*, *dp* is $kpq\alpha_{(P)}$ and *dr* is $krs\alpha_{(R)}$. The expected change in the genotypic mean of the hybrid is

$$\Delta\overline{X}_{Hyb} = 2k\alpha_{(P)}\alpha_{(R)}(pq + rs) + (p - r)(2kpq\alpha_{(P)}\beta_{(R)} - 2krs\alpha_{(R)}\beta_{(P)}),$$

and the expected change in the mean of the synthetic variety is

$$\Delta\overline{X}_{Syn} = (kpq\alpha_{(P)} + krs\alpha_{(R)})(\alpha_{(P)} + \alpha_{(R)} - ((3/4)(p - r)^2(\gamma_{(P)} + \gamma_{(R)}))).$$

Thus, this interpopulation improvement procedure is a methodology which encompasses all combinations of the intrapopulation breeding procedures of chapter 2 except topcrosses. If both base populations are selected for the same trait with the same intrapopulation breeding method, the attributes, difficulties, and relative effectiveness described in the summary of chapter 2 would apply. If different intrapopulation breeding methods are used on the base populations, the expected change would be intermediate to the exclusive use of either intrapopulation breeding procedure.

Concurrent Topcrosses (CT)

With this breeding method, populations *P* and *R* are improved by use of a topcross method of breeding (TX, TXPX, or TXFS). Each population is crossed to a common tester population, *U*. Individuals or polycrossed families are selected on the basis of the performance of topcross progeny. The use of a common tester is not required but does minimize the number of parameters.

The equation for the change in the genotypic mean of the hybrid by use of TX selection on both base populations is

$$\Delta\bar{X}_{\mathrm{Hyb}_{(TX)}} = kpq(\alpha_{(U)} + (p-u)\beta_{(U)})(\alpha_{(R)} + (p-r)\beta_{(R)}) + krs(\alpha_{(U)} + (r-u)\beta_{(U)})(\alpha_{(P)} - (p-r)\beta_{(P)}),$$

and the change in the mean of the synthetic variety is

$$\Delta\bar{X}_{\mathrm{Syn}_{(TX)}} = [kpq(1/2)(\alpha_{(U)} + (p-u)\beta_{(U)}) + krs(1/2)(\alpha_{(U)} + (r-u)\beta_{(U)})][(\alpha_{(P)} + \alpha_{(R)} - ((3/4)(p-r)^2(\gamma_{(P)} + \gamma_{(R)}))].$$

Selection with TXPX or TXFS instead of TX reduces the gain by one-half.

Reciprocal Recurrent Selection (RRS)

With this breeding method, populations *P* and *R* are evaluated on the basis of the performance of topcross progenies, but the populations are used reciprocally as the tester population (Comstock et al. *1949*). That is, population *R* is the tester population for population *P*, and *P* is the tester population for *R*. The selected parents or polycrossed families in the base populations are combined to produce the new hybrid or synthetic variety.

The change in the genotypic mean of the hybrid with RRS procedure selection of parent plants is

$$\Delta\bar{X}_{\mathrm{Hyb}} = krs[\alpha_{(P)} + (r-p)\beta_{(P)}]^2 + kpq[\alpha_{(R)} + (p-r)\beta_{(R)}]^2,$$

and the change in the genotypic mean of the synthetic variety is

$$\Delta\bar{X}_{\mathrm{Syn}} = [(kpq/2)(\alpha_{(R)} + (p-r)\beta_{(R)}) + (krs/2)(\alpha_{(P)} + (r-p)\beta_{(P)})][\alpha_{(P)} + \alpha_{(R)} - ((3/4)(p-r)^2(\gamma_{(P)} + \gamma_{(R)}].$$

The selection of polycrossed progenies or full-sibs instead of the parents will reduce the above predictive equations by one-half.

Comparison of Interpopulation Breeding Procedures

As the breeding procedures become more involved, expectation equations become more complex, and the comparisons are much more difficult and require deterministic simulation. Comparisons of interpopulation improvement methods are meaningful between methods with common generation times and other attributes, such as selection of various progenies or parental plants. To make such a comparison, the mode of genic action must be defined in advance. One such comparison study now has been completed (Rowe and Hill *1981*).

The comparison was among HSPT with the SC procedure, TX selection with CT procedure, and parental plant selection, TX equivalent, with RRS procedure. Four types of genetic action were investigated: additive, monoplex

dominance, duplex dominance, and one type of overdominance. Comparisons among breeding methods were made for each type of genic action.

For the comparison, we assigned genotypic values to each genotype reflecting the genetic model, and the population effects were solved in terms of h, an arbitrary constant for trait expression (table 12). Expressions were developed for the change in genotypic mean of a two-population synthetic as a function of h, assuming constant selection pressure k.

Table 12.—Genotypic values and parameters for genetic models

Genotype and parameter	Genetic model[1]			
	Additive	Monoplex dominance	Duplex dominance	Over-dominance
BBBB	$4h$	h	h	0
BBBb	$3h$	h	h	$3h$
BBbb	$2h$	h	h	$4h$
Bbbb	h	h	0	$3h$
bbbb	0	0	0	0
Additive (α)	h	q^3h	$3pq^2h$	$3(p-q)h$
Digenic (β)	0	$-q^2h$	$q(1-3p)h$	$-2h$
Trigenic (γ)	0	qh	$(1-3q)h$	0
Quadrigenic (δ)	0	$-h$	$3h$	0

[1] h is an arbitrary constant, p and q are frequencies of alleles "*B*" and "*b*," respectively.

With additive genetic action, all procedures had the same predicted change of the population mean $\Delta\overline{X} = kh^2(pq + rs)$.

The equations for the effect of selection, assuming monoplex dominance, appear in table 13. The equation for SC response is also a component common to RRS and CT equations. The RRS equation contains two differences of squares, $s^2 - q^2$ and $q^2 - s^2$, one of which must be a negative value if not zero. When the differences are zero, this equation simplifies to the SC equation. With CT selection, the difference in squares, $v^2 - q^2$ and $v^2 - s^2$, could both be positive values if $v > s$ and $v > q$. Rowe and Hill (*1981*) showed that CT was superior to either RRS or SC if the right tester population were used. The frequency of b must be greater in the tester than in P or R.

Assumptions of duplex dominance and overdominance resulted in very complex response equations (table 14 and 15) and no generalities about superiority of any procedure was possible. With overdominance, response to selection was negative for some allele frequencies with SC and CT selection, but not with RRS. With the more complicated genetic situations, three-dimensional plots of expected response to selection facilitated comparisons. (See Rowe and Hill *1981*.)

Table 13.—Equations for the change of the mean genotypic value of the 2-population synthetic for SC, RRS, and CT selection methods, assuming only monoplex dominance gene action

Selection method	Response equation[1]
SC	$\Delta\bar{X} = kh^2(pq^4 + rs^4)J$
RRS	$\Delta\bar{X} = kh^2(pq^4 + rs^4 + pq^2(s^2 - q^2) + rs^2(q^2 - s^2))J$
CT	$\Delta\bar{X} = kh^2(pq^4 + rs^4 + pq^2(v^2 - q^2) + rs^2(v^2 - s^2))J$
	$J = (q^3 + s^3) - (3/4)(p - r)^2(q + s)$

[1] *k*, *h*, *p*, *r*, *u*, *q*, *s*, and *v* are, respectively, ratio of selection differential to phenotypic variance, arbitrary constant of trait, frequency of allele "*B*," same, same, frequency of allele "*b*," same, and same.

Table 14.—Equations for the change of the mean genotypic value of the 2-population synthetic for SC, RRS, and CT selection methods, assuming only duplex dominance gene action

Selection method	Response equation[1]
SC	$\Delta\bar{X} = kh^2(3p^2q^3 + 3r^2s^3)J$
RRS	$\Delta\bar{X} = kh^2(3p^2q^3 + 3r^2s^3 + pqrs(2 - 3p) + pqrs(2 - 3r) + p^2q(s - 3q^2) + r^2s(q - 3s^2))J$
CT	$\Delta\bar{X} = kh^2(3p^2q^3 + 3r^2s^3 + pquv(2 - 3p) + rsuv(2 - 3r) + p^2q(v - 3q^2) + r^2s(v - 3s^2))J$
	$J = 3pq^2 + 3rs^2 - (3/4)(p - r)^2(2 - 3q - 3s)$

[1] *k*, *h*, *p*, *r*, *q*, *s*, and *v* are, respectively, ratio of selection differential to phenotypic variance, arbitrary constant for trait, frequency of allele "*B*," same, same, frequency of allele "*b*," same, and same.

Table 15.—Equations for the change of the mean genotypic value of the 2-population synthetic for SC, RRS, and CT selection methods, assuming only overdominance gene action

Selection method	Response equation[1]
SC	$\Delta\bar{X} = kh^2(pq(3-6p)+rs(3-6r))J$
RRS	$\Delta\bar{X} = kh^2(pq(3-6p)+rs(3-6r)+4pq(p-r)+4rs(r-p))J$
CT	$\Delta\bar{X} = kh^2(pq(3-6p)+rs(3-6r)+4pq(p-u)+4rs(r-v))J$
	$J = 3((1-2p)+(1-2r))$

[1] k, h, p, r, u, q, s, and v are, respectively, ratio of selection differential to phenotypic variance, arbitrary constant for trait, frequency of allele "*B*," same, same, frequency of allele "*b*," same, and same.

Summary

The obvious complexity of the theoretical equations for interpopulation breeding, even with the assumptions for genetic simplicity, limits generalities about the relative effectiveness of the breeding schemes. The change in the genotypic mean of the hybrid with selection is a function of allele frequencies in each population involved, the additive and digenic components of the base populations, and the genetic components of *dp* and *dr*. The change in the genotypic mean of the synthetic is a function of allele frequencies in each population, the additive and trigenic components of the base populations, and the genetic components of *dp* and *dr*.

In any particular case, it is not obvious whether the digenic and trigenic components would increase or decrease the rate of gain over that observed with only additive genetic effects. Concurrent Topcrossing is not directly comparable to either the Select and Combine or Reciprocal Recurrent Selection method because of the genetic effects of the tester population, *U*. Nor is it obvious whether the mean of the hybrid or the synthetic variety changes more rapidly with selection.

The alternative approach is deterministic simulation, as described briefly in the previous section. Even in that simulation, the number of assumptions was increased and the generalities were diminished and reduced in scope. Simulation appears to be the only useful solution to many of the current questions in the theory of interpopulation improvement and is expected to be much used in subsequent theoretical research.

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