Estimation of genetic components of variance in the interpopulation formed by crossing two maize synthetics, BS10 and BS11

by

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1977

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My purpose in this study was to estimate the amount and type of genetic variability in the interpopulation formed by crossing two maize synthetics, BS10 and BS11; and to compute the expected genetic change in the two populations and their cross due to interpopulation selection, using the variance estimates obtained. I also compared the predicted response with the observed gain.

I used two mating designs, the nested (Design I) and crossed classification (Design II) mating schemes, and a combination of the two designs (Design I,II). Genetic parameters were defined in terms of the reference population which is the interpopulation formed from paired crossing of random individuals in the two parent populations. Genetic variability in the interpopulation was partitioned into additive and dominance components with their interactions with the environment.

Data were collected on eight traits in four environments with two replications in each environment. Days to silk was measured in only three environments. Design components of

variance from the combined analysis of variance were used to estimate the interpopulation variance components. In the interpopulation, additive genetic variance ($\sigma^2_{A_{(12)}}$) was the most important genetic variance component for all nine traits. Dominance variance ($\sigma^2_{D_{(12)}}$) was about half the additive variance for tiller number and yield. For the remaining seven traits, $\sigma^2_{D_{(12)}}$ was about one-quarter or less, the amount of $\sigma^2_{A_{(12)}}$. Except for yield, estimates of additive x environment interaction variance ($\sigma^2_{AE_{(12)}}$) were much lower than their corresponding $\sigma^2_{A_{(12)}}$ for all traits. There was no definite trend in estimates of dominance x environmental interaction variance ($\sigma^2_{DE_{(12)}}$) when compared with corresponding $\sigma^2_{D_{(12)}}$. Estimates of variance components in the combined DI,II tend to be biased towards the DI estimates. Although DI,II estimates were associated with higher standard errors, than the estimates of individual DI and DII, the error variance estimates were relatively reduced by combining the DI and DII mating schemes.

The three correlation coefficients among traits using variance and covariance components estimated from the three procedures, DI, DII, and DI,II, were highest for ear height with yield. Ear diameter and kernel depth were equally most correlated with yield.

There was good agreement, trend-wise, between the expected and observed gain from selection for yield. After three cycles of reciprocal full-sib selection, there was an observed gain of 22% in the $C_3 \times C_3$ interpopulation compared to the

original C_0 x C_0 population cross; the predicted genetic gain was 37%. An observed gain of 17% in the two parent populations also was realized from the three selection cycles.

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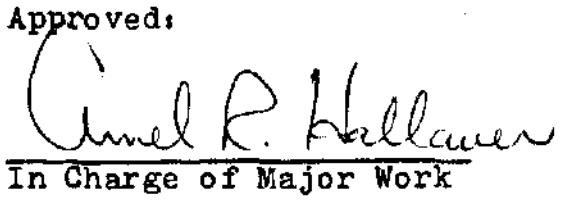
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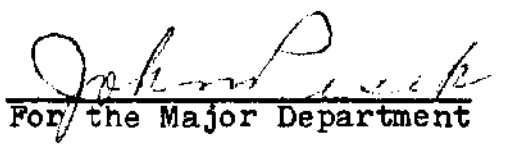
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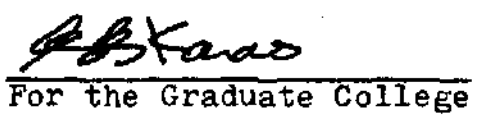
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I. INTRODUCTION

The development and production of high performing and acceptable maize varieties, single-cross hybrids, variety crosses, or multiple-cross hybrids (synthetics or composites) are, and will continue to be, the principal objective of the maize breeder. The classical breeding method of introduction, hybridization, and selection has been utilized to produce the single-, three-way-, and double-cross hybrids. This method involved using highly inbred lines that had been tested for their performance in topcrosses with various forms of testers. The elite lines having good combining abilities were ultimately selected, crossed, and tested to determine the high yielding hybrids. The flaw with this classical method, which still accounts for most of the single-cross hybrids used in the majority of maize producing countries of the world today, is the long time, in years, necessary for achieving the goal, coupled with the number and related types of hybrids (in terms of parent-line genotypes) developed. The method also has other problems because of the effect of inbreeding depression in the formation of inbred lines, and the restriction of the genetic base of the hybrid. The latter factor makes the hybrids easily vulnerable to epidemics of diseases and insect pests.

In the 1950's, "recurrent selection" breeding schemes were developed in an attempt to remove some of the restrictions

encountered by the earlier breeding methods. Recurrent selection is a procedure that maintains genetic variability in the selection population, and permits, at the same time, the frequency of desirable genes and gene combinations to be increased by recombination of selected genotypes. Four broad groups of recurrent selection in crop development have been described, based on identification of the recombination units: simple recurrent selection, recurrent selection for general combining ability, recurrent selection for specific combining ability, and reciprocal recurrent selection. Reciprocal recurrent selection was designed to capitalize on all types of gene actions, namely, additive, dominance, and epistatic gene actions.

In the course of improving the recurrent selection methodology and philosophy, the comprehensive breeding system was developed. The system provides for efficient population improvement, as well as generating better performing genotypes from which desirable progenies are selected for further inbreeding, evaluation, and selection. As a modification of this system and the reciprocal recurrent selection method, the "Reciprocal Full-sib Selection" method was proposed, which evaluates full-sib rather than half-sib progenies in a population cross. It is a breeding procedure for concurrent population improvement and hybrid development. This selection method has been proved effective in producing high yielding inbred lines <u>per se</u> and in hybrid combinations. An understanding of

its effectiveness is necessary in order to sufficiently utilize its full potentials. A close examination of the amount and type of genetic variability present in the population cross that results from generating reciprocal full-sib progenies is required for achieving the desired objective.

There are, therefore, three main objectives in my study: (1) to obtain estimates of the amounts of genetic variability (additive and nonadditive) in the interpopulation by use of two mating designs, the nested (Design I) and the crossed-classification (Design II) mating schemes, separately and combined; (2) to utilize the estimates obtained for computing the expected genetic change (progress from selection) in the two populations due to interpopulation selection for yield; and (3) to compare the predicted response with the observed gain.

II. LITERATURE REVIEW

A. Reciprocal Full-sib Selection (RFS): An Interpopulation Recurrent Selection Method

Reciprocal recurrent selection (RRS) is a breeding and selection technique for improvement of populations proposed by Comstock, Robinson, and Harvey (1949) for the development of commercial hybrids. The scheme evaluates half-sib progenies and, theoretically, is supposed to be effective irrespective of the type and level of gene action predominating. It requires two populations to be used as the base (foundation) materials. These populations could be two open-pollinated varieties, two synthetics, or the F_2 generation plants of two simple crosses used in producing double-crosses. Whatever populations are used, they must be heterogeneous enough to have a substantial amount of genetic variability available for selection.

In principle, objectives of most selection programs are taking advantage of available resources, both in plant materials and environments, to enhance progress from selection. Hallauer (1967a and 1967b) and Lonnquist and Williams (1967) utilized such an advantage in the prolific trait of maize and proposed a modification of the RRS. In this modification, called Reciprocal Full-sib Selection (RFS) (Hallauer and Eberhart, 1970), two maize populations with two or more ears per plant are used as foundation stocks (although single-eared

maize populations also can be used, but with a loss in amount of progress); and the materials evaluated are full-sib progenies, rather than the half-sib progenies as in RRS. The RFS scheme is thus a breeding procedure designed for concurrent population improvement, inbred line development, and efficient development of single-cross hybrids. The mechanics of the population improvement phase are similar to that outlined by Comstock et al. (1949). The details of the breeding scheme can be outlined (as illustrated by Hallauer, 1973) as follows:

Cycle 0:

Season 1: Make S_0 x S_0 individual plant crosses in paired rows consisting of the two populations A and B. At the same time, self each of the plants used in the paired crosses to produce intrapopulation S_1 inbred lines.

Season 2: Evaluate S_0 x S_0 plant crosses in replicated yield trials in more than one environment.

Season 3: Recombine S_1 seeds for each population of the highest performing and selected S_0 x S_0 pairs. This forms the base population for the next cycle.

Cycle 1: Repeat procedures in cycle 0. The "Population Improvement Phase" of the RFS described above takes 2 years to accomplish with a winter nursery. The evaluation of the full-sib progenies (S_0 x S_0 plant-to-plant crosses) provides

information for the selection of parents to be recombined in the two populations, to form the next cycle population, and, also, early test information is obtained for the development of new inbred lines and hybrids. The parents of the superior yielding progenies, therefore, are recombined to form the next selection cycle for each of the two parental populations; and planted ear-to-row in the corresponding pairs for continued selfing and crossing for developing new lines and testing for new single-cross hybrids. This latter section is the second phase of the RFS scheme--"Single-cross Hybrid Development Phase", described below:

Season 1: Make S_0 x S_0 individual plant crosses. Self each plant of each pair to obtain S_1 inbred lines.

Season 2: Evaluate S_0 x S_0 plant crosses in replicated yield tests in at least two environments. In the breeding nursery, grow the pairs of S_1 progenies and make S_1 x S_1 plant crosses; also, self the S_1 line plants to obtain S_2 lines.

Season 3: Evaluate the selected S_1 x S_1 plant crosses in replicated yield trials. Grow the pairs of S_2 progenies and make S_2 x S_2 plant crosses. Self S_2 lines to obtain S_3 lines.

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Season 6: Evaluate S_4 x S_4 plant crosses in replicated yield trials. Select the best plant cross and increase component S_4 lines for single-cross hybrid production.

This phase is repeated every cycle of recurrent selection. The techniques used to produce the single crosses (full-sib progenies) and selfed seed on the same plants were described by Hallauer (1967a, 1967b) and Lonnquist and Williams (1967).

Progress in plant breeding using recurrent selection methods is dependent on two main basic factors: (1) the amount of genetic variability in the base populations; and (2) the efficiency of the selection procedures used. There is no information, yet, in the literature on the type and amount of progress expected from the RFS procedure. However, the effectiveness of the selection method has been indicated from experimental results by Hallauer (1973), Hoegemeyer and Hallauer (1976), and from computer model simulation studies by Jones, Compton, and Gardner (1971).

Jones et al. (1971), comparing RRS against RFS, found that RFS gave greater response than did RRS throughout the selection period, particularly at lower selection intensities and when environmental variance was large relative to the total genetic variance. However, Jones et al. (1971) pointed out, from their theoretical reasoning, that because only half as many families must be evaluated in RFS as for RRS to maintain the same effective population size in each population,

hence, the selection intensity is doubled. This doubling of the selection intensity offsets the increase in phenotypic variance for full-sib as against half-sib families. It should be indicated, though, that progress is faster and the procedure (RFS) is simpler (than RRS) when at least one population produces two ears per plant.

Hallauer (1973) reported a significant improvement in the populations per se after one cycle of selection. Using two maize populations, BSTE (BS10) and PHPRC (BS11), he obtained a 14.8% and 18.7%, respectively, higher yield values for the C_1 population than their respective C_0 populations. The fact that the yield trials serve as early testing of the lines and hybrids, the population improvement via full-sib reciprocal recurrent selection (Hallauer, 1973) is also an indication of its potential usefulness and effectiveness.

In the development of high yielding inbred lines, the RFS procedure has also been shown to be very effective. Hoegemeyer and Hallauer (1976) concluded from their study that this method of selection developed an elite group of lines having high specific combining ability with its tested mate and also high general combining ability with other elite lines, with a minimum of testing. Studying the development of single crosses of maize from selection among and within full-sib families in two populations (BS10 and BS11), they observed: (1) that interpopulation crosses averaged 5.8 q/ha (7.4%) greater yields than intrapopulation crosses, and (2) the

crosses of selected lines yielded 8.7 q/ha (11.2%) more than crosses of unselected lines.

B. Interpopulation Genetic Parameters

Some information is available in the literature on the amount and types of genetic variability present in interpopulations (two-population cross). Estimates of such genetic parameters are necessary for the evaluation of the effectiveness and progress expected from breeding procedures that involve two populations and their crosses. The development of the quantitative genetic theory required for the characterization of hybrid populations produced by the crossing of two individuals from two separate populations has received little attention. Most of the estimates from interpopulation genetic studies have been interpreted on the basis of intrapopulation theory and assumptions. This procedure can only prove adequate if the two populations have almost similar alleles with the same gene frequencies.

Comstock et al. (1949) proposed the first breeding procedure that would make maximum use of both general and specific combining ability; it was called reciprocal recurrent selection (RRS). They made theoretical comparisons among the RRS, recurrent selection for combining ability and recurrent selection for specific combining ability proposed by Hull (1945), using relative changes in gene frequencies. In interpopulation breeding procedures, such as the RRS and RFS, understand-

ing the population behavior under selection requires a knowledge of the genetic relationship and parameterization of the different types of relatives generated. Weir and Cockerham (1976) presented and discussed a two-locus theory that could be used to provide means and variances for a two-locus quantitative model of gene effects in a population cross to determine the covariance of relatives in the interpopulation.

Estimates of genetic variance components in interpopulations have been reported by Robinson and Comstock (1955); Robinson, Khalil, Comstock and Cockerham (1958); Compton, Gardner and Lonnquist (1965); and Stuber (1965). Robinson and Comstock (1955) presented estimates of additive genetic variance (σ_A^2), dominance variance (σ_D^2) and level of dominance (σ_D^2/σ_A^2) for yield in hybrid populations. They conducted their studies with progenies developed from the F_2 generation of four hybrid populations derived from single crosses of inbred lines. They also studied the effects of selection for yield improvement. They established that:

1. Genes affecting yield of grain, for the most part, show dominance ranging from partial to complete. If there is overdominance, it exists at only a portion of the effective loci.
2. The indicated level of dominance of genes in some F_2 generations of hybrids developed from crossing isogenic lines is different from that indicated in open-pollinated varieties. The upward bias due to

linkage effects in the estimates of dominance variance in hybrid populations is suggested to account for pseudo-overdominance. This could be observed from the decreasing trend in level of dominance with selection.

3. An appreciable amount of additive genetic variance and little or no dominance variance seems to remain in the populations after three cycles of selection.

Robinson et al. (1958) used Design I to study the genetic variation and heterosis in two maize populations, 'Jarvis' and 'Indian Chief', and their variety cross. They mated a random plant, as male, from one variety to four random plants, as females, from the second variety to obtain the interpopulation. They concluded that the component of variance due to genetic differences between male parents was greater within the varieties than in the variety cross. The same trend was shown for the female parents mated to the same male. Their results agreed with a genetic model assuming additive gene effects with partial to complete dominance (as shown in a previous study by Robinson and Comstock, 1955), and no epistasis or multiple alleles. Their average σ^2_m and $\sigma^2_{f/m}$ values for the population crosses (and reciprocals) was .00049 and .00083, respectively, with no significant difference between the values for crosses and reciprocals. They also observed greater heterosis in the variety crosses than the midparent by about 20%.

In a similar study, Compton, Gardner and Lonnquist (1965)

reported genetic variances observed among full-sib and half-sib families within the varieties 'Golden Republic' and 'Barber Reid', and the intervariety crosses. From the Design I scheme, the genetic variances they estimated from intervariety families tended to be higher than those from their respective intravariety families. Compton et al.'s (1965) observations are in contrast to those found by Robinson et al. (1958); the ratio of intravariety genetic variances to intervariety genetic variances also were found to be less than 1.0. Their average interpopulation estimates for σ^2_m and $\sigma^2_{f/m}$ for yield were also greater (.00241 and .00314, respectively) than those obtained by Robinson et al. (1958). Their results, however, showed consistency with a model of additive gene action with no more than partial to complete dominance and no epistasis, which agrees with the earlier studies of Robinson and Comstock (1955) and Robinson et al. (1958).

Stuber (1965) characterized genetic variation in a population F_1 cross of two maize varieties 'Jarvis' and 'Indian Chief'. Using Designs I and II, separately, he partitioned the interpopulation genetic variability into additive, dominance, and epistatic components by use of a factorial approach. For the genetic variation in yield in the interpopulation, Stuber (1965) indicated that the magnitudes of the additive variance and the dominance variance differed very little. This insignificant difference in additive and dominance variances for yield does not hold for other traits studied. The

additive variance was found to be greater than dominance variance for ear number and days to tassel. For number of tillers, plant height, and ear height, most of the interpopulation genetic variability was accounted for by additive effects, while the dominance variation was insignificant.

Most studies involving problems of the type of gene action in populations and their crosses have indicated little or no significance of epistatic effects on observed hybrid vigor. Studies of Robinson et al. (1958), Compton et al. (1965), and Stuber (1965) have indicated negligible or no epistatic genetic variability in the traits studied in population crosses. In populations per se, Eberhart (1961) using 'Indian Chief' and 'Jarvis' varieties and Silva (1974) in BSSS also found no intrapopulation epistatic effects.

Evidence for either the presence or the absence of epistatic gene action in interpopulations has been presented from studies on heterosis for yield. Pollak (1956) working with three interpopulations formed by crossing three varieties of maize, 'Jarvis', 'Indian Chief', and 'Weekly', found that the F_2 generation and the average of the two backcrosses were generally intermediate in performance with respect to the average of the varieties and the F_1 for yield and three yield components. He concluded that there is no evidence for the presence of epistasis in his experiment. In the cross of 'Jarvis' and 'Indian Chief', however, Prairie (1957) detected the presence of epistasis as suggested by significant devia-

tions from his model which included only additive and dominance effects.

The nondetection of significant epistasis in these studies does not mean the complete absence of epistatic effects of genes in these populations and their crosses. Several factors, including nullifying effects of positive and negative epistasis, may be responsible for the results obtained. However, it can logically and naturally be assumed that epistasis is accountable for some portion (no matter how minor) of any observed heterosis in interpopulation hybrid progenies. This assumption should be closer to being valid if the populations are widely divergent in their genetic make-up, with dissimilar alleles and different gene frequencies.

III. MATERIALS AND METHODS

A. Plant Materials and Genetic Designs

The materials used in this study were derived from two 2-eared maize populations, Iowa Two-ear Synthetic (BSTE) BS10 and Pioneer Two-ear Composite (PHPRS) BS11. These two genetically broad-based populations have been used in the reciprocal full-sib selection program (Hallauer, 1967a and 1973). BSTE was developed by W. A. Russell of the corn breeding group of the Iowa State University Agriculture and Home Economics Experiment Station by recombining 10 Corn Belt inbred lines that expressed strong two-ear tendencies. PHPRC was developed by W. L. Brown of the Pioneer Hi-Bred International, Inc., Johnston, Iowa, by crossing Caribbean and Southern United States germplasm with Corn Belt inbred lines. Both reference populations were planted in isolation and selection was practiced for the strong expression of two ears per plant before starting the reciprocal full-sib program.

Hallauer (1967a) initiated the reciprocal full-sib selection program in 1963 using BSTE and PHPRC. In 1963, 144 S_0 x S_0 plant crosses (cryptic double crosses) were produced in the C_0 populations of BSTE and PHPRC. Because the plants were two-eared, each plant involved in a cross was also selfed. During each selection cycle, in order to ensure enough good seed set for yield trial of the interpopulation full-sib (S_0 x S_0) crosses and recombination and maintenance of the

parents (S_1 lines) of selected full-sib progeny crosses, the second ears were crossed the first day of pollination and the top ears were selfed on the second day. The original S_0 plant genotypes from each base population were maintained by single-seed descent to develop a random, unselected group of inbred lines for BSTE and PHPRC. Each line was maintained by single-seed descent until the S_7 generation. In the S_7 generation all plants in a 25-plant row were self-pollinated to provide sufficient seed for experimental purposes. Because of the procedure used in their development, the S_7 lines were a random and unselected sample of inbred lines from BSTE and PHPRC. Hence the S_7 lines could be used to obtain estimates of genetic variation in the populations.

For the purpose of my study, I used two mating designs, Design I and Design II. The Design I and Design II mating designs were proposed by Comstock and Robinson (1948) to generate half-sib and full-sib progenies for evaluation and estimation of genetic components of variance.

For the Design I mating scheme, random S_0 plants of the C_0 populations from BSTE and PHPRC were used. One randomly selected male plant from BSTE was mated to six random female plants from PHPRC. Enough sets were produced to have 20 sets, each set including four males with each male mated to six females. Each set therefore included 24 full-sib progenies of the Design I mating design. At planting, the females were first planted while those plants to be used as males were

delayed. This delayed planting provided the stagger effect for pollination nick and to minimize the effects of assortative mating for flowering. To minimize possible maternal and paternal effects, half the crosses using S_0 plants of BSTE as males were made with S_0 plants of PHPRC as females, and the other half of the crosses were made using S_0 plants of PHPRC as males with S_0 plants of BSTE as females. Therefore, all crosses were not made using one population as males and the other population as females. We had, therefore, 10 sets of the crosses BSTE (S_0) x PHPRC (S_0) and 10 sets of the crosses PHPRC (S_0) x BSTE (S_0) were obtained, where the female was the second population listed. Since 20 sets were made, each including four males mated to six females, 480 full-sib progenies were thus produced for evaluation. From this Design I, since S_0 plants from both BSTE and PHPRC were used in the nested crosses, the coefficient of inbreeding of the parents used was $F = 0$.

For the Design II mating system, 144 S_0 plants from each of the original populations of BSTE and PHPRC were inbred to the seventh generation ($F \simeq 1$). For the purpose of my study, 80 S_7 inbred lines from BSTE and 80 S_7 inbred lines from PHPRC were used. The matings were made using sets of four random S_7 lines from BSTE and four random S_7 lines from PHPRC in the pattern shown.

	BSTE			
PHPRC	1'	2'	3'	4'
1	1 x 1'	1 x 2'	1 x 3'	1 x 4'
2	2 x 1'	2 x 2'	2 x 3'	2 x 4'
3	3 x 1'	3 x 2'	3 x 3'	3 x 4'
4	4 x 1'	4 x 2'	4 x 3'	4 x 4'

Each set, therefore, had 16 full-sib progenies. Twenty sets of such crosses were made; pooling over sets, 320 full-sib progenies were then available for evaluation.

The evaluation of full-sib progenies provides information for the selection of parents to be recombined to form the next cycle population. Also, early test information is obtained for the development of new hybrids and synthetics. At the end of each cycle, therefore, parents (S_1 lines) of identified superior yielding progenies (S_0 x S_0 crosses) are recombined to form the next selection cycle for each of the two parental populations. Four cycles of the population improvement phase of the selection scheme were completed in 1974 winter nursery. In the C_0 populations inbreeding of the 144 S_0 plants was continued and plant-to-plant crosses produced and tested through the S_5 generation. In the S_5 generation, 18 selections from PHPRC C_0 and 24 selections from BSTE C_0 were recombined in 1969 to form the C_1 population for each variety (PHPRC(FR)C_1

and BSTE(FR)C_1). The C_2 populations of PHPRC and BSTE (PHPRC(FR)C_2 and BSTE(FR)C_2) were developed from the S_1 progenies of the superior S_0 x S_0 crosses of the C_1 populations. Twenty S_1 progenies were used for recombination in 1971. To form the C_3 populations of PHPRC and BSTE, 20 pairs of S_1 progenies were selected for recombination in 1974. The selection of recombined S_1 progenies to produce PHPRC(FR)C_3 and BSTE(FR)C_3 was not only based on yield performance of the (C_2) S_0 x S_0 crosses but also on their insect resistance ratings and stalk quality and those of the S_1 lines per se.

As the populations have been improved, new advanced generations have been generated. Variety crosses between the original population and the improved generations were made in the pattern shown: C_0 x C_0; C_1 x C_1; C_2 x C_2 and C_3 x C_3. To obtain information on the amount of progress made by reciprocal full-sib selection in the PHPRC and BSTE, the original population (C_0), the improved population cycles (C_1, C_2, C_3) and their crosses were evaluated in agronomic trials in 1974.

B. Experimental Design

For the evaluation trials, I had a total of 800 full-sib progenies generated from the two types of mating designs: 480 crosses from Design I and 320 crosses from Design II. The 800 full-sib progenies were grown in four experiments: two experiments near Ames and Ankeny in 1973; one experiment near Ames in 1974; and one experiment near Ames in 1975.

The materials for evaluation were assigned to 20 sets for each mating design and were grouped in 20 blocks for the field design. Each block containing 40 full-sib families from both designs was replicated twice in each experiment. Each of the 20 blocks, therefore, included one set of 16 Design II full-sib progenies, and one set of 24 Design I full-sib progenies, the replications for each set being adjacent to each other as shown:

Block 1 (= Set 1)		- - -	Block 20 (= Set 20)
Rep 1	Rep 2		
24 DI plots (F = 0)	16 DII plots (F = 1)		
16 DII plots (F = 1)	24 DI plots (F = 0)		

The layout of the entries obtained from the Design I and Design II designs in each replication was randomly arranged. The plots within each design in each of the replications were also randomly allocated. This experimental design and field layout provides the conditions under which the assumptions used in combining both mating designs I and II in one evaluation experiment could be valid. The assumptions used in comparing progenies with different inbreeding coefficients (F) in this experiment are:

1. That the plot-to-plot environmental variation is the same for both Design I and Design II progenies.
2. That the within-plot environmental variance is also the same for the two types of progenies.

Each experiment was treated as a different environment. In each environment, each progeny-entry was grown in a single-row plot of 17 plants. The plants were spaced 25.4 cm apart within the plot and the distance between the plots was 101.6 cm. The plots were overplanted to ensure good stand. At the 5 to 7 leaf stage, plots were thinned to 17 plants per plot. This gave a population density of 38,734 plants per hectare. Missing hills were not compensated and only 10 competitive plants were used in measurements for all traits.

Data were taken for days to silk, ear height, number of tillers, height of tallest tiller, ear length, ear diameter, cob diameter, kernel depth and total grain weight (yield). Measurements were taken for all traits except days to silk in all four environments, on plot mean basis. Days to silk data were collected at the three environments located near Ames. The nine traits were measured as follows:

1. Ear height: The distance from ground level to the node bearing the primary (1st) ear, measured to the nearest centimeter.

2. Days to silk: The date 50% of the plants in a plot showed silk was recorded on a tag. The number of days to 50% silking was the period between July 1 and the date of 50% silking.

3. Number of tillers: The number of tillers produced per plot were counted and divided by the number of competitive plants per plot to find the average number of tillers.

4. Height of tallest tiller: The distance from ground level to the base of the flag leaf of the tallest tiller of each competitive plant was measured and recorded to the nearest 10 centimeters.

5. Ear length: The total length of all harvested primary ears was measured to the nearest 0.5 centimeter and divided by the number of primary ears harvested to obtain the average ear length.

6. Ear diameter: The total diameter of all harvested primary ears was measured to the nearest 0.5 centimeter and divided by the number of primary ears harvested to obtain the average ear diameter.

7. Cob diameter: The total diameter of all cobs, measured to the nearest 0.5 centimeter, divided by the total number of cobs in a plot.

8. Kernel depth: The difference between the ear diameter and the cob diameter.

9. Yield: The total shelled grain weight (in grams) of

IV. GENETIC STATISTICAL THEORY AND ANALYSES

The two mating designs used in my study, Design I and Design II of Comstock and Robinson (1948), and the form of experimental design used to evaluate the full-sib progenies developed from them, provided the information for the estimation of components of variance and covariance of the relatives. Because the inbreeding coefficient of the parents used in the two mating designs was different (F = 0 for Design I and F = 1 for Design II), the coefficients of the genetic components of variance were different for the two mating designs. In defining the genetic parameters from the statistical theory and analyses developed in this section, the reference population will be the interpopulation generated from crossing random individuals from the two parent populations. Estimates of genetic parameters also were obtained from combined Designs I and II (DI, II). Mean squares and mean products from the combined analyses for each mating design were combined into one matrix for the estimation of genetic variances and covariances, respectively. The estimates of genetic variances and covariances obtained will be used to (1) calculate correlation coefficients between pairs of the traits studied, and (2) predict response to selection using interpopulation (reciprocal full-sib) recurrent selection method.

Data for each trait for each mating design were analyzed by randomized complete block design for each set and pooled

over sets within each experiment. Experimental results also were combined over the four experiments (environments) for each trait to obtain the combined analysis of variance. The partitioning and estimation of variance components, covariances, correlations, and prediction of genetic gain from selection were done for each of the Design I and Design II progenies, and for the two designs combined (DI,II) at the two different inbreeding levels.

A. Genetic Variation in the Interpopulation

The partitioning of the hereditary variance in the interpopulation is done using the factorial approach by Cockerham (1954) for diploid populations. As a modification, I will consider only additive (linear) and dominance (quadratic) effects and variances and their interactions with environment. I am assuming epistasis is negligible or absent. Two independent loci, each with two alleles A_iA_k and B_jB_l, from both populations are considered. Individuals from the interpopulation will have genotypes of the form A_iB_j/A_kB_l with allelic frequencies $P,P'/(1-P),(1-P')$. The general two-locus model (not including epistasis) for such a situation is:

$$G_{kl}^{ij} = \mu_o + a_i + a_k + b_j + b_l + d_{ik}^{a} + d_{jl}^{b} \quad ,$$

where

G_{kl}^{ij} is the genotypic value of an individual,

a_i, a_k are the additive effects for the alleles at the A locus,

b_j, b_l are the additive effects for the alleles at the B locus,

d^a_{ik} is the dominance effect at the A locus, and

d^b_{jl} is the dominance effect at the B locus.

A pair of genes is equivalent by descent if they both descend from genes on one initial gamete. Allelic genes which are equivalent by descent are therefore identical by descent (Weir and Cockerham, 1976). For a random individual with genes a_1b_1/a_2b_2 in the interpopulation, there are six possible pairs of genes, and fifteen possible arrangements in gametes of the initial genes from which a_1, b_1, a_2, b_2 are descended. When each locus is assumed to be equally inbred and if the coupling and repulsion double heterozygotes are phenotypically identical, the number of arrangements reduces to nine genotypes (Table 1). In Table 1, Y's indicate the genetic values and f's indicate the relative frequencies of the respective genotypes. The probabilities of the nine arrangements sum to one.

When alleles and nonalleles are independent as they should be coming from two different populations, they are uncorrelated in whatever values they assume with regard to traits to which they contribute. If the alleles are uncorrelated, their frequencies are also uncorrelated. If the frequencies of the alleles at one locus are uncorrelated with the frequencies at a second locus in the parent populations, their frequencies will be uncorrelated in the interpopulation. Thus, the total variance among the genetic values (Y's) in Table 1 can be

Table 1. Genetic values (Y) and relative frequencies (f) of the nine genotypes for two independent loci, each with two alleles

$A_iA_iB_jB_j$	$A_iA_iB_jB_1$	$A_iA_iB_1B_1$	A_iA_i——
Y_{22}[a]	Y_{21}	Y_{20}	$Y_{2.}$[b]
f_{22}	f_{21}	f_{20}	$f_{2.}$
$A_iA_kB_jB_j$	$A_iA_kB_jB_1$	$A_iA_kB_1B_1$	A_iA_k——
Y_{12}	Y_{11}	Y_{10}	$Y_{1.}$
f_{12}	f_{11}	f_{10}	$f_{1.}$
$A_kA_kB_jB_j$	$A_kA_kB_jB_1$	$A_kA_kB_1B_1$	A_kA_k——
Y_{02}	Y_{01}	Y_{00}	$Y_{0.}$
f_{02}	f_{01}	f_{00}	$f_{0.}$
$-B_jB_j$	$-B_jB_1$	$-B_1B_1$	
$Y_{.2}$	$Y_{.1}$	$Y_{.0}$	$Y_{..}$
$f_{.2}$	$f_{.1}$	$f_{.0}$	$f_{..} = 1$

[a]First subscript indicates number of favorable alleles at locus A; second subscript indicates number of favorable alleles at locus B.

[b]A dot (.) means marginal mean or marginal frequency.

partitioned into a marginal variance for the A locus (i.e., variance among the row means), a marginal variance for the B locus (i.e., variance among the column means) and an interaction variance (epistatic variance), which I will not be considering in this study. Each of the marginal variances can be partitioned into a linear (additive) and a quadratic (dominance) variance. Statistically, Table 1 is a linear and quadratic treatment of a 3^2 factorial where each of the partitions corresponds to one of the eight degrees of freedom. The loci are the factors and each factor has three levels represented by the three genotypic combinations that are possible with two alleles. Since the frequencies at different loci are uncorrelated, there will be no effect of linkage on the partitioning of variances.

In partitioning the genetic variances, a method similar to orthogonal polynomials described by Anderson and Bancroft (1952) will be used. Eight orthogonal scales (Table 2) are used to compute a portion of the total variance for each degree of freedom, from the nine possible genotypic combinations in the 3^2 factorial table (Table 1). The particular set of eight scales or eight partitions of variance chosen is one of several that could be used. Certain requirements, in the form of restrictions, are needed for the use of the orthogonal scales because the joint or interaction variances are not equal but result from the products of the marginal frequencies. The restrictions are:

Table 2. Genetic values (Y), relative frequencies (f) and form of the four out of eight general orthogonal scales used to partition the genetic variance among the nine genotypes (Cockerham, 1954)

Scale (W)	Genotypes								
	$A_iA_iB_jB_j$	$A_iA_iB_jB_1$	$A_iA_iB_1B_1$	$A_iA_kB_jB_j$	$A_iA_kB_jB_1$	$A_iA_kB_1B_1$	$A_kA_kB_jB_j$	$A_kA_kB_jB_1$	$A_kA_kB_1B_1$
Y	Y_{22}	Y_{21}	Y_{20}	Y_{12}	Y_{11}	Y_{10}	Y_{02}	Y_{01}	Y_{00}
f	f_{22}	f_{21}	f_{20}	f_{12}	f_{11}	f_{10}	f_{02}	f_{01}	f_{00}
W_1	$2v$[a]	$2v$	$2v$	$v-u$	$v-u$	$v-u$	$-2u$	$-2u$	$-2u$
W_2	$\frac{1}{f_{2.}}$	$\frac{1}{f_{2.}}$	$\frac{1}{f_{2.}}$	$-\frac{2}{f_{1.}}$	$-\frac{2}{f_{1.}}$	$-\frac{2}{f_{1.}}$	$\frac{1}{f_{0.}}$	$\frac{1}{f_{0.}}$	$\frac{1}{f_{0.}}$
W_3	$2y$	$y-x$	$-2x$	$2y$	$y-x$	$-2x$	$2y$	$y-x$	$-2x$
W_4	$\frac{1}{f_{.2}}$	$-\frac{2}{f_{.1}}$	$\frac{1}{f_{.0}}$	$\frac{1}{f_{.2}}$	$-\frac{2}{f_{.1}}$	$\frac{1}{f_{.0}}$	$\frac{1}{f_{.2}}$	$-\frac{2}{f_{.1}}$	$\frac{1}{f_{.0}}$

[a] $u = f_{2.} + f_{1./2}$ = gene frequency of A_i; $v = 1 - u$ = gene frequency of A_k; $x = f_{.2} + f_{.1/2}$ = gene frequency of B_j; $y = 1 - x$ = gene frequency of B_1.

(1) $\sum_{i,j} f_{ij} W_{tij} = 0$, and

(2) $\sum_{i,j} f_{ij} W_{tij} W_{t'ij} = 0$,

where W_t is any particular scale, and

f is any relative frequency for any particular genotype.

The first restriction insures that deviations around the mean are compared. The second restriction insures that the comparisons are orthogonal, that is, are uncorrelated.

The first two scales, W_1 and W_2 in Table 2, are concerned only with the marginal variance (both additive and dominance) for the A locus. Similarly, the second two scales, W_3 and W_4, represent the marginal variance (both additive and dominance) for the B locus. The other remaining four scales, W_5, W_6, W_7, and W_8 relate to the interactions among the two loci (i.e., epistasis), and will not be considered here and in subsequent tables of scales because of my previous assumption of no epistasis.

Table 3 shows the eight orthogonal scales for two loci in the interpopulation I am considering. The gene frequencies of gene A_i in parent populations 1 and 2 are represented by p and q, respectively, and those of the second gene A_k in the pair are represented by (1-p) and (1-q), respectively. Similarly p' and q' represent frequencies of gene B_j, and (1-p') and (1-q') represent frequencies of gene B_l, respectively,

Genotypes		
$A_iA_kB_jB_j$	$A_iA_jB_kB_l$	$A_iA_kB_lB_l$
Y_{12}	Y_{11}	Y_{10}
$(p+q-2pq)$ $p'q'$	$(p+q-2pq)$ $(p'+q'-2p'q')$	$(p+q-2pq)$ $(1-p')(1-q')$
$1-p-q$	$1-p-q$	$1-p-q$
$\frac{-2}{p(1-p)+q(1-q)}$	$\frac{-2}{p(1-p)+q(1-q)}$	$\frac{-2}{p(1-p)+q(1-q)}$
$2-p'-q'$	$1-p'-q'$	$-p'-q'$
$\frac{p'+q'-2p'q'}{p'q'[p'(1-p')+q'(1-q')]}$	$\frac{-2}{p'(1-p')+q'(1-q')}$	$\frac{p'+q'-2p'q'}{[p'(1-p')+q'(1-q')][(1-p')(1-q')]}$

Table 3. (Continued)

Scale (W)	Genotypes		
	$A_kA_kB_jB_j$	$A_kA_kB_jB_l$	$A_kA_kB_lB_l$
Y	Y_{02}	Y_{01}	Y_{00}
f	$(1-p)(1-q)$ $p'q'$	$(1-p)(1-q)$ $(p'+q'-2p'q')$	$(1-p)(1-q)$ $(1-p')(1-q')$
W_1	$-p-q$	$-p-q$	$-p-q$
W_2	$\frac{p+q-2pq}{[p(1-p)+q(1-q)]}$ $[(1-p)(1-q)]$	$\frac{p+q-2pq}{[p(1-p)+q(1-q)]}$ $[(1-p)(1-q)]$	$\frac{p+q-2pq}{[p(1-p)+q(1-q)]}$ $[(1-p)(1-q)]$
W_3	$2-p'-q'$	$1-p'-q'$	$-p'-q'$
W_4	$\frac{p'+q'-2p'q'}{p'q'[p'(1-p')+q'(1-q')]}$	$\frac{-2}{p'(1-p')+q'(1-q')}$	$\frac{p'+q'-2p'q'}{[p'(1-p')+q'(1-q')]}$ $[(1-p')(1-q')]$

in the two populations. If the frequencies of the genes considered for a particular locus are the same in the two populations, then the resulting interpopulation will be at Hardy-Weinberg equilibrium at that locus. If gene frequencies are not the same, equilibrium will only be reached after one generation of random mating the interpopulation.

The partition of the variance, σ_t^2, corresponding to any particular scale, W_t, is obtained from the equation by Cockerham (1954):

$$\sigma_t^2 = \left(\sum_{i,j} f_{ij} Y_{ij} W_{tij}\right)^2 / \sum_{i,j} f_{ij} W_{tij}^2 \quad ,$$

which, statistically, is

$$\sigma_t^2 = (\mathrm{Cov} Y W_t)^2 / \sigma_{W_t}^2 = \beta_{YW_t}^2 \sigma_{W_t}^2$$
$$= \rho_{YW_t}^2 \sigma_Y^2 \quad ,$$

where, Cov, β, and ρ are covariance, regression coefficient, and correlation coefficient, respectively. The t^{th} partition of the variance is, thus, the variance due to regression on the t^{th} orthogonal scale. Table 4 shows the theoretical partition of genetic variances in the interpopulation for four of the eight scales (epistasis assumed absent). The values in the table have been obtained by solving for σ_t^2 in Table 3. These values show an important point; the components of genetic variation in an interpopulation still depend, mainly, on the gene frequencies of the alleles coming from

Table 4. Partitions of the genetic variance in the interpopulation for two loci for four orthogonal scales

Scale	Partition of variance, σ_t^2
W_1 (additive at A locus)	$\dfrac{\left\{pq(2-p-q)(Y_{2.}-Y_{1.})+[p(1-p)+q(1-q)-pq(1-p-q)](Y_{1.}-Y_{0.})\right\}^2}{p(1-p)+q(1-q)}$
W_2 (dominance at A locus)	$\dfrac{pq(1-p)(1-q)(p+q-2pq)[(Y_{2.}-Y_{1.})-(Y_{1.}-Y_{0.})]^2}{p(1-p)(+q(1-q)}$
W_3 (additive at B locus)	$\dfrac{\left\{p'q'(2-p'q')(Y_{.2}-Y_{.1})+[p'(1-p')+q'(1-q')-p'q'(2-p'-q')](Y_{.1}-Y_{.0})\right\}^2}{p'(1-p')+q'(1-q')}$
W_4 (dominance at B locus)	$\dfrac{p'q'(1-p')(1-q')(p'+q'-2p'q')[(Y_{.2}-Y_{.1})-(Y_{.1}-Y_{.0})]^2}{p'(1-p')+q'(1-q')}$

independent loci in the two parent populations and the genotypic values of the resulting crossed progenies.

B. Covariances Between Relatives in the Interpopulation

The relations between relatives can be described in terms of the covariances between the components that make up the total genetic variation. This study focuses only on the genetic covariances between half-sibs and full-sibs in the population crosses. The orthogonal scales used in partitioning genetic variation (Tables 3 and 4) also will be used in obtaining the correlations between relatives in the interpopulation, as used by Cockerham (1954) for random mating populations and relatives from randomly mated inbred parents.

Let the genetic values for two relatives be Y and Y', and their orthogonal scales be W_t and W'_t, respectively. Assuming no change in gene frequencies in the interpopulation progenies (with one generation of random mating and the relatives in the same generation), relatives with the same genotypes will have the same genetic values and same scale. The covariance between Y and Y' could then be expressed as:

$$\text{Cov } YY' = \sum_{t,t'} \text{Cov}(\beta_{YW_t} W_t)(\beta_{Y'W'_{t'}} W'_{t'}) \quad ,$$

where $t,t' = 1 \ldots 4$

But $\sigma_t^2 = \beta_{YW_t}^2 \sigma_{W_t}^2 = \rho_{YW_t}^2 \sigma_Y^2$ (Section A) .

Therefore, $\text{Cov } YY' = \sum_{t,t'} (\beta_{YW_t} W_t)(\beta_{Y'W'_{t'}} W'_{t'})\sigma_t \sigma'_{t'}$.

Because the regression coefficients are constants and they do not affect the absolute value of the correlation coefficients,

$$\rho(\beta_{YW_t}W_t)(\beta_{Y'W'_t}W'_t) = \pm \rho W_r W'_t \quad .$$

Then

$$\text{Cov } YY' = \sum_{t,t'} \rho_{W_t W'_t} \sigma_t \sigma'_t \quad .$$

The result of the correlation between the four orthogonal scales of one relative and those of the other relative is shown in 4 x 4 table (Table 5). The complex computation leading to the simple result is given by Cockerham (1954) in the appendix to his paper. The covariances between full-sibs (offsprings with both parents in common) and half-sibs (offsprings with one parent in common) can be obtained from the joint distribution of the relatives in the interpopulation. From such distribution, Cockerham (1954) computed the covariances as follows:

At the A locus,

$\rho_{W_1 W_1'} = (1+F)/2$

$\rho_{W_2 W_2'} = (1+F)^2/4$, and

$\rho_{W_1 W_2'} = \rho_{W_2 W_1'} = 0$, where

F is the inbreeding coefficient for any level of inbreeding;

$\rho_{W_1 W_1'}$ is the correlation between the additive effects of full-sibs;

$\rho_{W_2 W_2'}$ is the correlation between the dominance deviation of full sibs; and the relationship

Table 5. Correlations between the four scales of one relative and the four scales of another relative

	W_1'	W_2'	W_3'	W_4'
W_1	$\rho_{W_1W_1'}$	$\rho_{W_1W_2'}$	0	0
W_2	$\rho_{W_2W_1'}$	$\rho_{W_2W_2'}$	0	0
W_3	0	0	$\rho_{W_3W_3'}$	$\rho_{W_3W_4'}$
W_4	0	0	$\rho_{W_4W_3'}$	$\rho_{W_4W_4'}$

$\rho_{W_1W_2'} = \rho_{W_2W_1'} = 0$ means that the additive effects of one full-sib are not correlated with the dominance deviations of the other full-sib.

Similarly, at the B locus,

$\rho_{W_3W_3'} = (1+F)/2$,

$\rho_{W_4W_4'} = (1+F)^2/4$, and

$\rho_{W_3W_4'} = \rho_{W_4W_3'} = 0$.

Analogously, for half-sibs, it was found that only the additive effects of the half-sibs were correlated, and this was $(1+F)/4)$.

The use of mating designs, which generates various types of relatives, has greatly enhanced estimation of components of genetic variances. To translate the covariances between

full-sibs and half-sibs into components of genetic variation, the population crosses were used as the reference populations. For such translations, certain basic assumptions were made, as in the case of intrapopulations by Comstock and Robinson (1952) and Cockerham (1963). In my study of the interpopulation, BSTE (BS10) x PHPRC (BS11), I will consider two levels of inbreeding ($F = 0$ and $F = 1$). If reciprocal effects are negligible or absent and if there are no environmental correlations among relatives (avoidable by randomization), the covariances among relatives can be directly translated into components of interpopulation genetic variances. Symbols used in subsequent expressions are defined as follows:

CovHS = covariance among half-sib relatives; and

CovFS = covariance among full-sib relatives.

Superscripts 0 and 1 refer to the levels of inbreeding of the parents used in the matings. Subscripts 1 and 2 refer to the mating design used.

With no inbreeding, $F = 0$, and when the common (male) parent of a half-sib family comes from population 1, the covariance among the half-sibs is:

$$\text{CovHS}^{0}_{12} = 1/4\ \sigma^2_{A_{12}} \quad .$$

Similarly, when the common parent comes from population 2, the covariance among the half-sibs is:

$$\text{CovHS}^{0}_{21} = 1/4\ \sigma^2_{A_{21}} \quad .$$

The interpopulation covariance among half-sibs becomes:

$$\text{CovHS}^0_{12} + \text{CovHS}^0_{21} = 1/4\ \sigma^2_{A_{12}} + 1/4\ \sigma^2_{A_{21}}$$

$$= 1/4(\sigma^2_{A_{12}} + \sigma^2_{A_{21}}) = 1/2\ \sigma^2_{A_{(12)}} \quad .$$

With the parents consisting entirely of nearly homozygous lines ($F \simeq 1$), and the common parent of a half-sib family coming from population 1, the covariance among the half-sibs is:

$$\text{CovHS}^1_{12} = 1/2\ \sigma^2_{A_{12}} \quad .$$

Similarly, with the common parent coming from population 2, the

$$\text{CovHS}^1_{21} = 1/2\ \sigma^2_{A_{21}} \quad .$$

The interpopulation covariance among half-sibs when there is complete inbreeding then becomes:

$$\text{CovHS}^1_{12} + \text{CovHS}^1_{21} = 1/2\ \sigma^2_{A_{12}} + 1/2\ \sigma^2_{A_{21}}$$

$$= 1/2(\sigma^2_{A_{12}} + \sigma^2_{A_{21}}) = \sigma^2_{A_{(12)}} \quad ; (\sigma^2_{A_{12}} = \sigma^2_{A_{21}}) \quad .$$

When the level of inbreeding in the two parent populations is near one ($F \simeq 1$), and there are no reciprocal differences,

$$\text{CovFS}^1_{12} = \text{CovFS}^1_{21} \quad .$$

The covariance among full-sibs is:

$$\text{CovFS}^1_{12} = \sigma^2_{A_{12}} + \sigma^2_{D_{12}} \quad , \text{ and}$$

$$\text{CovFS}^1_{21} = \sigma^2_{A_{21}} + \sigma^2_{D_{21}} \quad , \text{ and}$$

$$\sigma^2_{A_{12}} + \sigma^2_{D_{12}} = \sigma^2_{A_{21}} + \sigma^2_{D_{21}} \quad .$$

The interpopulation covariance among full-sibs will then be:

$$\sigma^2_{A_{(12)}} + \sigma^2_{D_{(12)}} \quad .$$

With no inbreeding in the parent populations (F = 0), the relationship is still:

$$CovFS^0_{12} = CovFS^0_{21} \quad .$$

But the covariance among full-sibs becomes:

$$CovFS^0_{12} = 1/2\ \sigma^2_{A_{12}} + 1/4\ \sigma^2_{D_{12}} \quad ,$$

(assuming no difference in gene frequencies in the two populations) and,

$$CovFS^0_{21} = 1/2\ \sigma^2_{A_{21}} + 1/4\ \sigma^2_{D_{21}} \quad ,$$

and,

$$1/2\ \sigma^2_{A_{12}} + 1/4\ \sigma^2_{D_{12}} = 1/2\ \sigma^2_{A_{21}} + 1/4\ \sigma^2_{D_{21}} \quad .$$

The interpopulation covariance among full-sibs will then be:

$$1/2\ \sigma^2_{A_{(12)}} + 1/4\ \sigma^2_{D_{(12)}} \quad .$$

C. Estimating Interpopulation Genetic Variance Components: Design I

The effects of locations and years as components of environment in relation to genotypes were discussed by Robinson and Moll (1959) and Comstock and Moll (1963). They showed that variety x location and variety x year effects were small relative to the three-way interaction: variety x location x year effects. Although the location and years effects may be confounded in the estimate of variety x location x year, the data were combined over all environments (all experiments in

this study) without partitioning for years and locations. However, to ascertain whether there are significant interaction effects, a general combined analysis of variance was computed. It included locations and years as sources of variation (Table 6); the procedure would indicate if the confounding by separate effects of years and locations is either negligible or important. All environments (locations and years) were considered random.

The complete model used for the analysis of variance pooled over sets and combined across environments is:

$$Y_{lsmfr} = \mu + E_l + S_s + (SE)_{sl} + R_{slr} + M_{sm} + F_{smf} + (ME)_{sml} + (FE)_{smfl} + e_{smflr} \quad ,$$

where

$l = 1,...4$ (environments),

$s = 1,.....20$ (sets),

$m = 1,...4$ (males),

$f = 1,....6$ (females per male), and

$r = 1,2$ (replications).

The components of the model are defined as:

Y_{lsmfr} = r^{th} observation of the crossed progeny mf of the m^{th} male and f^{th} female in the s^{th} set and l^{th} environment;

μ = overall mean;

E_l = effect of l^{th} environment;

S_s = effect of s^{th} set;

$(SE)_{sl}$ = effect due to the interaction of the s^{th} set

Table 6. Form of the combined analysis of variance for 800 full-sib progenies evaluated for two years in two locations

Source	d.f.
Locations (L)	l-1
Years (Y)	Y-1
L x Y	(l-1)(y-1)
Replications/L/Y	ly(r-1)
Progenies (P)	(p-1)
Sets (S)	(s-1)
P/S	s(p-1)
P x L	(p-1)(l-1)
P x Y	(p-1)(y-1)
P x L x Y	(p-1)(l-1)(y-1)
S x L	(s-1)(l-1)
P/S x L	s(p-1)(l-1)
P/S x L x Y	s(p-1)(l-1)(y-1)
Pooled error	ly(p-1)(r-1)
Total	lypr-1

and the l^{th} environment;

R_{slr} = effect of the r^{th} replication within the s^{th} set in the l^{th} environment;

M_{sm} = effect of m^{th} male in the s^{th} set;

F_{smf} = effect of f^{th} female within the m^{th} male in the s^{th} set;

$(ME)_{sml}$ = effect due to the interaction between m^{th} male in the s^{th} set and l^{th} environment;

$(FE)_{smfl}$ = effect due to the interaction between f^{th} female within m^{th} male in the s^{th} set and the l^{th} environment; and

e_{smflr} = random error of the r^{th} observation of the crossed progeny mf of the m^{th} male and f^{th} female in the s^{th} set within the l^{th} environment.

In analyzing for each set in one environment, the terms E, S and others involving them are removed from the model. Likewise, the analysis for all sets in one environment will not include all the terms involving E.

In computing the expectations of the mean squares (E.M.S.), males (M) and females within (F/M) males from the two populations, and the environments were considered random variables. The sources of variation among the interpopulation full-sib progenies in one set and pooled over sets are partitioned in Tables 7 and 8. The expected mean squares from Tables 7 and 8 were the same and the sources of variability, M and F/M, can be tested by the appropriate mean squares. The null hypothesis H_0: $\sigma_m^2 = 0$ can be tested for each set and all sets in one environment:

$F_{(n_1,n_2)} = \frac{M_{11}}{M_{12}}$, where n_1, n_2 are the degrees of freedom associated with M_{11} and M_{12}, respectively, in the analysis of variance for each set;

$F_{(n_4,n_5)} = \frac{M_{14}}{M_{15}}$, where n_4, n_5 are the degrees of freedom

Table 7. Design I: Form of the analysis of variance and expected mean squares (E.M.S.) for each set in one environment

Source	d.f.	M.S.	E.M.S.[a]
Replications	r-1		
Males (M)	m-1	M_{11}	$\sigma_1^2 + 2\sigma_{f/m}^2 + 12\sigma_m^2$
Females (F)/M	m(f-1)	M_{12}	$\sigma_1^2 + 2\sigma_{f/m}^2$
Error	(mf-1)(r-1)	M_{13}	σ_1^2
Total	mfr-1		

[a] σ_1^2 is the experimental error variance, $\sigma_{f/m}^2$ is the variance of female effects within males, σ_m^2 is the variance of male effects, and r is the number of replications (r = 2), m is the number of males (m = 4), and f is the number of females mated to each male (f = 6).

associated with M_{14} and M_{15}, respectively, for the pooled analysis of 20 sets in one environment. Likewise, the hypothesis H_0: $\sigma_{f/m}^2 = 0$ can be tested directly by F-tests:

$F = \frac{M_{12}}{M_{13}}$ for one set; and

$F = \frac{M_{14}}{M_{15}}$ for pooling of all sets in one environment. The ratios $F = \frac{M_{11}}{M_{12}}$ and $F = \frac{M_{14}}{M_{15}}$ test the presence of additive variance and/or additive types of epistatic variance, only. On the other hand, ratios of $F = \frac{M_{12}}{M_{13}}$ and $F = \frac{M_{15}}{M_{16}}$ test for all types of genetic variances including additive, dominance, and

Table 8. Design 1: Form of the analysis of variance and expected mean squares (E.M.S.) pooled for 20 sets in one environment

Source	d.f.[a]	M.S.	E.M.S.[b]
Sets (S)	s-1		
Replications/S	s(r-1)		
Males (M)/S	s(m-1)	M_{14}	$\sigma_1^2 + 2\sigma_{f/m}^2 + 12\sigma_m^2$
Females (F)/M/S	sm(f-1)	M_{15}	$\sigma_1^2 + 2\sigma_{f/m}^2$
Pooled error	s(mf-1)(r-1)	M_{16}	σ_1^2
Total	smfr-1		

[a] s represents sets (s = 20)

[b] Terms in the E.M.S. are defined in Table 7.

epistatic variances. For the assumption of no epistasis, the respective tests are for additive genetic and total genetic variance.

All estimates of variation obtained from Tables 7 and 8 are biased upward because the experiments were conducted in only one environment. The male components of variance, σ_m^2, arise not only from additive genetic variance, but also from an additional interaction of the additive genetic effects with the environment; that is, $\sigma_m^2 = \sigma_m^2 + \sigma_{ml}^2$. Similarly, $\sigma_{f/m}^2$ is an estimate of $\sigma_{f/m}^2 + \sigma_{f/ml}^2$. Realistic estimates of variance components unbiased by genotype x environment interactions,

however, were obtained by pooling the sets for one environment and combining the experimental results over all environments. The analyses of such procedures with the expectation of mean squares are presented in Tables 9 and 10.

Tests of significance of the mating design variance components that are of interest (σ^2_m, $\sigma^2_{f/m}$, σ^2_{ml} and $\sigma^2_{f/ml}$) can be made by use of the F-distribution in the combined analysis (Table 9). If the genotype x environment interactions are not significant, a more powerful test of significance for the components could be obtained from the pooled analysis of variance for all environments (Table 10). In the combined analysis, since some of the variance components require more than two mean squares for their estimation, exact F-tests are not possible. An exact F-test for the male component, σ^2_m, is therefore no longer available. Consequently, an approximation suggested by Cochran (1951) was used. Thus the male mean squares can be tested as:

$$F'(n_1', n_2') = \frac{M_{17} + M_{110}}{M_{18} + M_{19}}$$, where the appropriate degrees of freedom are estimated as:

$$n_i' = \frac{(\sum_i M_i)^2}{\sum_i \frac{M_i^2}{n_i}} \quad .$$

The female component, $\sigma^2_{f/m}$, can be tested with the exact F-test, $F = \frac{M_{18}}{M_{110}}$. Likewise, tests can be made for the inter-

Table 9. Design I: Form of the combined analysis of variance and expected mean squares (E.M.S.) over four environments for 20 sets

Source	d.f.[a]	M.S.	E.M.S.[b]
Environments (E)	l-1		
Sets (S)	s-1		
S x E	(l-1)(s-1)		
Replications/S/E	sl(r-1)		
Males (M)/S	s(m-1)	M_{17}	$\sigma_1^2 + 2\sigma_{f/ml}^2 + 12\sigma_{ml}^2 + 8\sigma_{f/m}^2 + 48\sigma_m^2$
Females (F)/M/S	sm(f-1)	M_{18}	$\sigma_1^2 + 2\sigma_{f/ml}^2 + 8\sigma_{f/m}^2$
Males/S x E	s(m-1)(l-1)	M_{19}	$\sigma_1^2 + 2\sigma_{f/ml}^2 + 12\sigma_{ml}^2$
Females/M/S x E	sm(f-1)(l-1)	M_{110}	$\sigma_1^2 + 2\sigma_{f/ml}^2$
Pooled error	sl(mf-1)(r-1)	M_{111}	σ_1^2
Total	mfrsl-1		

[a] l represents environments (l = 4).

[b] σ_{ml}^2 and $\sigma_{f/ml}^2$ are variances due to genotype x environment interactions for the males and females within males, respectively. Other terms are defined in Tables 7 and 8.

Table 10. Design I: Form of the pooled analysis of variance and expected mean squares (E.M.S.) over four environments for 20 sets

Source	d.f.	M.S.	E.M.S.[a]
Environments (E)	l-1		
Sets (S)	s-1		
S/E	l(s-1)		
Replications/S/E	sl(r-1)		
Males (M)/S	s(m-1)	M_{112}	$\sigma_1^2 + 2\sigma_{f/m/l}^2 + 12\sigma_{m/l}^2 + 8\sigma_{f/m}^2 + 48\sigma_m^2$
Females (F)/M/S	sm(f-1)	M_{113}	$\sigma_1^2 + 2\sigma_{f/m/l}^2 + 8\sigma_{f/m}^2$
Males/S/E	sl(m-1)	M_{114}	$\sigma_1^2 + 2\sigma_{f/m/l}^2 + 12\sigma_{m/l}^2$
Females/M/S/E	sml(f-1)	M_{115}	$\sigma_1^2 + 2\sigma_{f/m/l}^2$
Pooled error	sl(mf-1)r-1)	M_{116}	σ_1^2
Total	mfrsl-1		

[a] $\sigma_{f/m/l}^2$ and $\sigma_{m/l}^2$ are variances due to females within males within environments, and males within environments, respectively. Other terms are defined in Tables 7, 8, and 9.

action components, σ^2_{ml} and $\sigma^2_{f/ml}$, respectively, as:

$$F = \frac{M_{19}}{M_{110}} \quad \text{, and } F = \frac{M_{110}}{M_{111}} \quad .$$

A significant F-test of σ^2_{ml} would indicate the interaction of additive and/or additive type epistatic effects with environment. On the other hand, significant $\sigma^2_{f/ml}$ is indicative of the interaction of genotypic effects with the environment.

The mating design variance components were estimated from the linear functions of the appropriate mean squares. All of the four mating design variance components (σ^2_m, $\sigma^2_{f/m}$, σ^2_{ml} and $\sigma^2_{f/ml}$ could be estimated as shown:

$$\hat{\sigma}^2_m = \frac{M_{17} + M_{110} - M_{18} - M_{19}}{48} \quad ;$$

$$\hat{\sigma}^2_{f/m} = \frac{M_{18} - M_{110}}{8}$$

$$\hat{\sigma}^2_{ml} = \frac{M_{19} - M_{110}}{12} \quad ; \text{ and } \hat{\sigma}^2_{f/ml} = \frac{M_{110} - M_{111}}{2} \quad .$$

The standard error of an estimated variance component can be computed from an approximate variance of a linear function of independent mean squares. If $X = a_1M_1 + a_2M_2 + a_3M_3 + \ldots$, then, assuming normality and independence of the distribution:

$$\text{Var}(X) = 2 \sum_i a_i^2 \frac{M_i^2}{n_i+2} \quad ; \text{ where}$$

n_i denotes the degrees of freedom associated with M_i, and a_i is the coefficient associated with the appropriate variance in the expectation of the mean squares. For example, the

approximate variance of the estimate of σ_m^2 is:

$$\mathrm{Var}(\sigma_m^2) = \frac{2}{(48)^2}\left[\frac{M_{17}^2}{2+s(m-1)} + \frac{M_{110}^2}{2+sm(f-1)(l-1)} + \frac{M_{18}^2}{2+sm(f-1)} + \frac{M_{19}^2}{2+s(m-1)(l-1)}\right] \quad ;$$

and its standard error is:

$$\sqrt{\mathrm{Var}(\sigma_m^2)} \quad .$$

The nature of the mating designs I used makes it possible to estimate various covariances among relatives. It is, therefore, necessary to translate the mating design variance components into the proper covariances. For the Design I mating scheme under the random genetic model:

$$Y_{ijk} = \mu + M_i + F_{ij} + e_{ijk} \quad ,$$

where Y_{ijk} = k^{th} observation of the ij^{th} cross;

μ = general mean;

M_i = effect of the i^{th} male; i = 1, 2, 3, 4;

F_{ij} = effect of the j^{th} female within the i^{th} male; 1, 2, ..., 6;

e_{ijk} = deviation due to the k^{th} observation of the ij^{th} cross; k = 1, 2;

and $M_i \sim$ NID $(0,\sigma_m^2)$,

$F_{ij} \sim$ NID $(0,\sigma_{f/m}^2)$,

$e_{ijk} \sim$ NID $(0,\sigma_1^2)$, where

NID = normally and independently distributed.

From the pattern of mating, two types of offsprings result:

interpopulation full-sibs (FS), Y_{ijk} and $Y_{ijk'}$ ($k \neq k'$), and interpopulation half-sibs (HS), Y_{ijk} and $Y_{ij'k}$ ($j \neq j'$). The covariances between these two types of relatives (CovFS and CovHS) will be shown as follows:

$$\text{CovFS} = E[Y_{ijk}-E(Y_{ijk})][Y_{ijk'}-E(Y_{ijk'})] \quad \text{, where}$$

$E(Y_{ijk})$ = expectation of $Y_{ijk} = \mu$; also

$E(Y_{ijk'})$ = expectation of $Y_{ijk'} = \mu$. Therefore,

$$\text{CovFS} = E[\mu+M_i+F_{ij}+e_{ijk}-\mu][\mu+M_i+F_{ij}+e_{ijk'}-\mu]$$

$$= E[M_i+F_{ij}+e_{ijk}][M_i+F_{ij}+e_{ijk'}]$$

$$= E[M_i^2+F_{ij}^2+e_{ijk}\cdot e_{ijk'} + \text{cross products}].$$

Assuming independence of parameters in the genetic model, the expectations of cross products and $E(e_{ijk}\cdot e_{ijk'})$ will be zero. Therefore,

$$\text{CovFS} = E(M_i^2 + F_{ij}^2)$$

$$= \sigma_m^2 + \sigma_{f/m}^2 \quad .$$

Similarly,

$$\text{CovHS} = E[Y_{ijk}-E(Y_{ijk})][Y_{ij'k}-E(Y_{ij'k})]$$

$$= E[M_i+F_{ij}+e_{ijk}][M_i+F_{ij'}+e_{ij'k}]$$

$$= E[M_i^2+F_{ij}\cdot F_{ij'}+e_{ijk}\cdot e_{ij'k} + \text{cross products}]$$

$$= E[M_i^2]$$

$$= \sigma_m^2 \quad .$$

It then follows that:

σ^2_m = CovHS and $\sigma^2_{f/m}$ = CovFS - CovHS .

The interpopulation genetic interpretations for the covariances among full-sibs and half-sibs were presented in section IV. B. I have just shown that the mating design variance components (σ^2_m and $\sigma^2_{f/m}$) are functions of the full-sib and half-sib covariances. Thus, the design components of variance can be translated in terms of genetic variances in the interpopulation.

In my study, the reference population is the interpopulation resulting from crossing the two populations, BS10 x BS11. Following the procedure used in carrying out the design matings, as described in section III, the design components could be defined as:

$\sigma^2_{1\,m_{12}}$ and $\sigma^2_{f/m^1_{12}}$ are the male component and the female within male component of variance, respectively, from a Design I experiment (superscript) in which males from population 1 were mated to females from population 2 (subscripts); and

$\sigma^2_{1\,m_{21}}$ and $\sigma^2_{f/m^1_{21}}$ are the male component and the female within male component of variance, respectively, from a Design I experiment (superscripts) in which males from population 2 were mated to females from population 1 (subscripts).

Similarly, the genetic variance components could be defined as:

$\sigma^2_{A_{12}^1}$ and $\sigma^2_{A_{21}^1}$ are the additive genetic variance related to $\sigma^2_{m_{12}^1}$ and $\sigma^2_{m_{21}^1}$, respectively; and

$\sigma^2_{A_{(12)}^1}$ is the interpopulation additive genetic variance for Design I.

Thus, for Design I (F = 0), if gene frequencies in the two parent populations do not differ greatly (p = r and q = s), the interpopulation additive genetic variance is calculated as follows:

$$\sigma^2_{m_{12}^1} = \text{CovHS}^0_{12} = \tfrac{1}{2}\sigma^2_{A_{12}^1} = \tfrac{1}{4}\sigma^2_A \quad \text{, because}$$

$$\sigma^2_{m_{12}^1} = \tfrac{1}{2}pq[\alpha + (q-p)\alpha]^2 = \tfrac{1}{4}\sigma^2_A \quad ,$$

where α is the average effect of gene substitution. Similarly,

$$\sigma^2_{m_{21}^1} = \text{CovHS}^0_{21} = \tfrac{1}{2}\sigma^2_{A_{21}^1} = \tfrac{1}{4}\sigma^2_A \quad \text{, and}$$

$$\sigma^2_{m_{12}^1} + \sigma^2_{m_{21}^1} = \tfrac{1}{2}(\sigma^2_{A_{12}^1} + \sigma^2_{A_{21}^1}) = \tfrac{1}{2}\sigma^2_{A_{(12)}^1} \quad .$$

The dominance deviation is calculated as:

$$\sigma^2_{f/m_{12}^1} + \sigma^2_{f/m_{21}^1} - \sigma^2_{m_{12}^1} - \sigma^2_{m_{21}^1} \quad \text{, where}$$

$$\sigma^2_{f/m_{12}^1} = \text{CovFS}^0_{12} - \text{CovHS}^0_{12} = \tfrac{1}{4}\sigma^2_A + \tfrac{1}{4}\sigma^2_D$$

$$\sigma^2_{f/m_{21}^1} = \text{CovFS}^0_{21} - \text{CovHS}^0_{21} = \tfrac{1}{4}\sigma^2_A + \tfrac{1}{4}\sigma^2_D$$

$$= \text{CovFS}^0_{12} - \text{CovHS}^0_{12} + \text{CovFS}^0_{21} - \text{CovHS}^0_{21} - \text{CovHS}^0_{12} - \text{CovHS}^0_{21}$$

$$= \text{CovFS}^0_{12} + \text{CovFS}^0_{21} - \text{CovHS}^0_{12} - \text{CovHS}^0_{12} - \text{CovHS}^0_{21} - \text{CovHS}^0_{21}$$

$$= (\tfrac{1}{2}\sigma^2_{A^1_{12}} + \tfrac{1}{4}\sigma^2_{D^1_{12}}) + (\tfrac{1}{2}\sigma^2_{A^1_{21}} + \tfrac{1}{4}\sigma^2_{D^1_{21}}) - \tfrac{1}{4}\sigma^2_{A^1_{12}} - \tfrac{1}{4}\sigma^2_{A^1_{12}} - \tfrac{1}{4}\sigma^2_{A^1_{21}} - \tfrac{1}{4}\sigma^2_{A^1_{21}}$$

$$= \tfrac{1}{2}\sigma^2_{A^1_{(12)}} + \tfrac{1}{4}\sigma^2_{D^1_{(12)}} - (2)\tfrac{1}{4}\sigma^2_{A^1_{(12)}}$$

$$= \tfrac{1}{4}\sigma^2_{D^1_{(12)}} \quad .$$

The analysis for this study was done in line with the pattern of mating plants from the two populations. There were 20 sets of four males each mated to six females. Each set thus consisted of 24 interpopulation full-sib progenies. Sets 1 through 10 included full-sib progenies from the interpopulation cross BS10 (female) x BS11 (male); while sets 11 through 20 included full-sib progenies of the cross BS10 (male) x BS11 (female). In the combined and pooled analyses, the three resulting groups of sets were computed separately as sets 1 through 10, 11 through 20, and 1 through 20. This procedure is intended to achieve two things: (1) to identify the design variance components $\sigma^2_{m^1_{12}}$, $\sigma^2_{m^1_{21}}$, $\sigma^2_{f/m^1_{12}}$ and $\sigma^2_{f/m^1_{21}}$; and (2) to indicate the validity of the expression $\sigma^2_{m_{12}} + \sigma^2_{m_{21}} = \tfrac{1}{2}(\sigma^2_{A_{12}} + \sigma^2_{A_{21}}) = \tfrac{1}{2}\sigma^2_{A_{(12)}}$. If the two types of estimates are similar, it will be valid to sum them to obtain the interpopulation additive genetic variance $\sigma^2_{A_{(12)}}$. If, however, there are natural or reciprocal effects, as are expected due to the mating of different random males of one population to different random females of the other population, the two sets of design

component estimates $\sigma^2_{m_{12}}$, $\sigma^2_{f/m^1_{12}}$ and $\sigma^2_{m^1_{21}}$, $\sigma^2_{f/m^1_{21}}$ will be different. It could then follow that pooling the estimates in a complete combined analysis of sets 1 through 20 to give only one estimate of σ^2_m may be invalid.

D. Estimating Interpopulation Genetic Variance Components: Design II

For the design II mating scheme, the complete model used for the combined analysis of variance for all sets pooled is:

$$Y_{lsmfr} = \mu + E_l + S_s + (SE)_{sl} + R_{slr} + M_{sm} + F_{sf} + (MF)_{smf} + (ME)_{sml} + (FE)_{sfl} + (MFE)_{smfl} + e_{smflr},$$

where

$l = 1,....4$ (environments),

$s = 1,.....20$ (sets),

$m = 1,....4$ (males),

$f = 1,....4$ (females), and

$r = 1,2$ (replications).

Also,

Y_{lsmfr}, μ, E_l, S_s, $(SE)_{sl}$, R_{slr}, M_{sm}, and $(ME)_{sml}$ are as defined for Design I model. The remaining terms in the model are:

F_{sf} = effect of the f^{th} female in the s^{th} set;

$(MF)_{smf}$ = effect due to the interaction of the m^{th} male with the f^{th} female in the s^{th} set;

$(FE)_{sfl}$ = effect due to the interaction of the f^{th} female in the s^{th} set with the l^{th} environment;

$(MFE)_{smfl}$ = effect due to the interaction of the m^{th} male and f^{th} female with the 1^{th} environment; and

e_{smflr} = random error in the r^{th} observation of the cross of m^{th} male with the f^{th} female in the s^{th} set within the 1^{th} environment.

All parameters in the model, except μ, are NID $(0,\sigma^2$ parameter).

The analyses of variance were carried out using the same procedures as in the Design I. For the analysis in one environment for one set, the terms E, S and others involving these terms were removed from the model. In the same way, the analysis for all sets pooled in one environment will not include the term E. For the computation of the expected mean squares, males, females and the environments were considered random variables.

The forms of the analysis of variance and their expected mean squares for each set and all sets pooled in one environment are shown in Tables 11 and 12. The null hypotheses for the mating design variance components generated in the expectation of the mean squares can be tested using appropriate F-tests.

As indicated for the Design I, all estimates obtained from each set and all sets pooled in one environment will be biased upwards by the genotype x environment interaction effects, which cannot be separated. However, if all sets are pooled within an environment and combined over all environments

Table 11. Design II: Form of the analysis of variance and expected mean squares (E.M.S.) for each set in one environment

Source	d.f.	M.S.	E.M.S.[a]
Replications	r-1		
Males (M)	m-1	M_{21}	$\sigma_2^2 + 2\sigma_{mf}^2 + 8\sigma_m^2$
Females (F)	f-1	M_{22}	$\sigma_2^2 + 2\sigma_{mf}^2 + 8\sigma_f^2$
M x F	(m-1)(f-1)	M_{23}	$\sigma_2^2 + 2\sigma_{mf}^2$
Error	(mf-1)(r-1)	M_{24}	σ_2^2
Total	mfr-1		

[a] σ_2^2 is the experimental error variance, σ_{mf}^2 is the interaction variance between males and females, σ_f^2 is the genetic variance among females, σ_m^2 is the genetic variance among males, and r is the number of replications, m is number of males, and f is number of females.

unbiased estimates of the mating design variance components will be obtained. In this case, the genotypic, environmental, and genotype x environment interaction variances are estimable. Because the same full-sib progenies were used as entries in the four experiments, the data for all the sets could be combined and pooled over the environments. The forms of the combined and pooled analyses of variance and their mean square expectations (E.M.S.) are shown in Tables 13 and 14. In the combined analysis, as was indicated for Design I, only an approximate

Table 12. Design II: Form of the analysis of variance and expected mean squares (E.M.S.) for 20 sets pooled in one environment

Source	d.f.[a]	M.S.	E.M.S.[b]
Sets	s-1		
Replications/sets	s(r-1)		
Males (M)/sets	s(m-1)	M_{25}	$\sigma_2^2 + 2\sigma_{mf}^2 + 8\sigma_m^2$
Females (F)/sets	s(f-1)	M_{26}	$\sigma_2^2 + 2\sigma_{mf}^2 + 8\sigma_f^2$
M x F/sets	s(m-1)(f-1)	M_{27}	$\sigma_2^2 + 2\sigma_{mf}^2$
Pooled error	s(mf-1)(r-1)	M_{28}	σ_2^2
Total	smfr-1		

[a] s represents the number of sets.

[b] All terms in the E.M.S. are defined in Table 11.

test could be used to test for the presence and significance of the additive types of genetic variation. These are, however, complex and indirect.

From the expectations of mean squares and using the mean squares in Table 13, the presence of additive and/or additive types of epistatic variance can be tested using both σ_m^2 and σ_f^2 components with Cochran's (1951) approximation. Thus:

$$F_{(n_1,n_2)} = \frac{M_{29} + M_{214}}{M_{211} + M_{212}} \quad , \text{ where } n_i = \frac{(\sum_i M_i)^2}{\sum_i (\frac{M_i}{n_i})^2} \quad ;$$

and

Table 13. Design II: Form of the combined analysis of variance and expected mean squares (E.M.S.) over four environments for 20 sets

Source	d.f.[a]	M.S.	E.M.S.[b]
Environments (E)	l-1		
Sets (S)	s-1		
S x E	(l-1)(s-1)		
Replications/S/E	sl(r-1)		
Males (M)/S	s(m-1)	M_{29}	$\sigma_2^2 + 2\sigma_{mfl}^2 + 8\sigma_{mf}^2 + 8\sigma_{ml}^2 + 32\sigma_m^2$
Females (F)/S	s(f-1)	M_{210}	$\sigma_2^2 + 2\sigma_{mfl}^2 + 8\sigma_{mf}^2 + 8\sigma_{fl}^2 + 32\sigma_f^2$
M x F/S	s(m-1)(f-1)	M_{211}	$\sigma_2^2 + 2\sigma_{mfl}^2 + 8\sigma_{mf}^2$
M/S x E	s(m-1)(l-1)	M_{212}	$\sigma_2^2 + 2\sigma_{fml}^2 + 8\sigma_{ml}^2$
F/S x E	s(f-1)(l-1)	M_{213}	$\sigma_2^2 + 2\sigma_{fml}^2 + 8\sigma_{fl}^2$
M x F/S x E	s(m-1)(f-1)(l-1)	M_{214}	$\sigma_2^2 + 2\sigma_{fml}^2$
Pooled error	sl(mf-1)(r-1)	M_{215}	σ_2^2
Total	slmfr-1		

[a] l represents the number of environments.

[b] σ_{ml}^2 and σ_{fl}^2 are variances due to genotype x environment interactions for the males and females, respectively. σ_{mfl}^2 is the three-way interaction variance between males, females, and the environments.

Table 14. Design II: Form of the pooled analysis of variance and expected mean squares (E.M.S.) across four environments for 20 sets

Source	d.f.	M.S.	E.M.S.[a]
Environments (E)	l-1		
Sets (S)	s-1		
S/E	l(s-1)		
Replications/S/E	sl(r-1)		
Males (M)/S	s(m-1)	M_{216}	$\sigma_2^2 + 2\sigma_{mf/l}^2 + 8\sigma_{mf}^2 + 8\sigma_{m/l}^2 + 32\sigma_m^2$
Females (F)/S	s(f-1)	M_{217}	$\sigma_2^2 + 2\sigma_{fm/l}^2 + 8\sigma_{mf}^2 + 8\sigma_{f/l}^2 + 32\sigma_f^2$
M x F/S	s(f-1)	M_{218}	$\sigma_2^2 + 2\sigma_{mf/l}^2 + 8\sigma_{mf}^2$
M/S/E	sl(m-1)	M_{219}	$\sigma_2^2 + 2\sigma_{mf/l}^2 + 8\sigma_{m/l}^2$
F/S/E	sl(f-1)	M_{220}	$\sigma_2^2 + 2\sigma_{mf/l}^2 + 8\sigma_{f/l}^2$
M x F/S/E	sl(m-1)(f-1)	M_{221}	$\sigma_2^2 + 2\sigma_{mf/l}^2$
Pooled error	sl(mf-1)(r-1)	M_{222}	σ_2^2
Total	slmfr-1		

[a] $\sigma_{m/l}^2$, $\sigma_{f/l}^2$, and $\sigma_{mf/l}^2$ are the variances due to males within environments, females within environments, and the interaction of males x females within the environment, respectively. The components have been defined in Tables 11-13.

$$F_{(n_1,n_2)} = \frac{M_{210} + M_{214}}{M_{211} + M_{213}} \quad .$$

M_i represents the mean square and n_i represents the respective degrees of freedom. Other mating design variance components can be directly tested using the mean squares and their expectations. Thus, for

$$H_0: \quad \sigma^2_{mf} = 0, \; F_{(n_1,n_2)} = \frac{M_{211}}{M_{214}} \quad ,$$

where $n_1 = s(m-1)(f-1)$ and $n_2 = s(m-1)(f-1)(l-1)$. This would be the test for dominance and/or dominant types of epistasis. Similarly, for

$$H_0: \quad \sigma^2_{ml} = 0, \text{ the test is } F_{(n_1,n_2)} = \frac{M_{212}}{M_{214}} \quad ; \text{ and for}$$

$$H_0: \quad \sigma^2_{fl} = 0, \text{ the test is } F_{(n_1,n_2)} = \frac{M_{213}}{M_{214}} \quad .$$

These two F-tests would test the presence of interaction of additive and/or additive type epistasis with environment. Finally, the interaction of dominance effects with environment can be tested with the null hypothesis,

$$H_0: \quad \sigma^2_{mfl} = 0, \text{ and the test is } F_{(n_1,n_2)} = \frac{M_{214}}{M_{215}} \quad .$$

By pooling the mean squares for M/S x E and F/S x E, a more powerful test of significance for σ^2_{ml} and σ^2_{fl} could be made because their expectations are the same. However, if the interaction estimates are not significant, a more powerful test for the male (σ^2_m) and female (σ^2_f) sources of variation and the

interaction between them could be obtained by pooling all the sets within all the environments, as shown in Table 14.

The Design II mating scheme also makes it possible to obtain correlations among the different types of relatives that result. It is, therefore, possible to relate the design variance components to the covariances between the relatives. These relationships for the interpopulation are shown to be:

$$\sigma^2_m = \text{CovHS}_{12} \; ; \quad \sigma^2_f = \text{CovHS}_{21} \; , \quad \text{and}$$

$$\sigma^2_{mf} = \text{CovFS} - (\text{CovHS}_{12} + \text{CovHS}_{21}) \; .$$

As was shown in section IV B, these design variance components can be translated in terms of interpopulation genetic variance components via the covariances among relatives. I will first define the design components from the interpopulation:

$\sigma^2_{m_1}{}^2$ and $\sigma^2_{f_2}{}^2$ are the male and female components of variance, respectively, from a Design II experiment (superscripts) with the males from population 1 and the females from population 2 (subscripts).

$\sigma^2_{m_2}{}^2$ and $\sigma^2_{f_1}{}^2$ are the male and female components of variance, respectively, from a Design II experiment (superscripts) with the males from population 2 and the females from population 1 (subscripts).

σ^2_{mf} denotes the male x female component of variance.

The inbreeding coefficient of inbred lines used for the Design II interpopulation crosses was $F \simeq 1$. This coefficient appears as the superscript on the designation of relatives. The mating design components of variance can now be translated in terms of interpopulation genetic variance components, as shown in section IV B, thus:

$$\sigma^2_{m_1 2} = \sigma^2_{m_2 2} = \sigma^2_{m 2} \text{ (since inbreds were used as parents, } F \simeq 1).$$

Also,

$$\sigma^2_{f_1 2} = \sigma^2_{f_2 2} = \sigma^2_{f 2} \text{ , and}$$

$$\begin{aligned} \sigma^2_{m 2} + \sigma^2_{f 2} &= \text{CovHS}^1_{12} + \text{CovHS}^1_{21} \\ &= \tfrac{1}{2}\sigma^2_A + \tfrac{1}{4}\sigma^2_{AA} + \tfrac{1}{2}\sigma^2_A + \tfrac{1}{4}\sigma^2_{AA} \\ &= \sigma^2_A + \tfrac{1}{2}\sigma^2_{AA} \\ &= \sigma^2_A \text{ , assuming no epistasis.} \end{aligned}$$

Therefore:

$$\sigma^2_{m 2} = \sigma^2_{f 2} = \tfrac{1}{2}\sigma^2_A \quad .$$

The dominance deviation can be estimated as:

$$\begin{aligned} \sigma^2_{mf 2} &= \text{CovFS}^1 - \text{CovHS}^1_{12} - \text{CovHS}^1_{21} \\ &\quad (\text{CovFS}^1_{12} = \text{CovFS}^1_{21} = \text{CovFS}^1) \\ &= \sigma^2_A + \sigma^2_D - \tfrac{1}{2}\sigma^2_A - \tfrac{1}{2}\sigma^2_A \\ &= \sigma^2_D \quad . \end{aligned}$$

E. Mating Designs I and II Combined: Estimation of Variance Components

In sections IV A to IV D, the interpopulation components of variance in the expectations of mean squares from the analysis of variance (Tables 7-14) were translated in terms of covariances between relatives generated from the population cross. The translation of covariances between relatives (full-sibs and half-sibs) into genetic variances have been shown previously for the interpopulation, using mating Design I and Design II, respectively. For the combined mating Design I and II estimates, mean squares from the analysis of variance are used as functions of genetic and environmental variances.

The genetic model I am using in this study involves only additive genetic and dominance variances. Using matrix notation and combining the mean squares from Design I and Design II interpopulation experiments in the same matrix, the translation of the mean squares in terms of genetic and environmental variances for the model used can be achieved. Table 15 shows the matrix of translation of the mean squares in 2 groups of 10 sets (Design I) and one group of 20 sets (Design II); all were pooled and combined over four environments, in terms of genetic, environmental and genetic by environmental variances. In Table 15, therefore, there are 17 equations to be solved and six parameters to be estimated. The parameters to be estimated include:

A = additive genetic variance;

Table 15. Matrix of mean squares for 2 groups of 10 sets (DI) and one group of 20 sets (DII) pooled over sets and combined over four environments. Translations are in terms of genetic, environmental, and genetic x environmental variances of the expected mean squares[a]

	M.S.	A	D	AE	DE	E_I	E_{II}
		Design I					
		(BS10♀ x BS11♂)					
Males (M)/sets (S)	M_{17}	14.0	2.0	3.5	0.5	1.0	0.0
Females (F)/M/S	M_{18}	2.0	2.0	0.5	0.5	1.0	0.0
Males/S x environments (E)	M_{19}	0.0	0.0	3.5	0.5	1.0	0.0
Females /M/S x E	M_{110}	0.0	0.0	0.5	0.5	1.0	0.0
Pooled error	M_{111}	0.0	0.0	0.0	0.0	1.0	0.0
		(BS10♂ x BS11♀)					
Males (M)/sets (S)	M_{17}	14.0	2.0	3.5	0.5	1.0	0.0
Females (F)/M/S	M_{18}	2.0	2.0	0.5	0.5	1.0	0.0
Males/S x environments (E)	M_{19}	0.0	0.0	3.5	0.5	1.0	0.0
Females/M/S x E	M_{110}	0.0	0.0	0.5	0.5	1.0	0.0
Pooled error	M_{111}	0.0	0.0	0.0	0.0	1.0	0.0

[a] A = interpopulation additive genetic variance; D = interpopulation dominance deviation; AE = interpopulation additive x environmental interaction variance; DE = interpopulation dominance x environmental interaction variance; E_I = interpopulation environmental variance for Design I; E_{II} = interpopulation environmental variance for Design II.

Table 15. (Continued)

	M.S.	A	D	AE	DE	E_I	E_{II}
		Design II					
Males (M)/sets (S)	M_{29}	16.0	8.0	4.0	2.0	0.0	1.0
Females (F)/S	M_{210}	16.0	8.0	4.0	2.0	0.0	1.0
M x F/S	M_{211}	0.0	8.0	0.0	2.0	0.0	1.0
M/S x environments (E)	M_{212}	0.0	0.0	4.0	2.0	0.0	1.0
F/S x E	M_{213}	0.0	0.0	4.0	2.0	0.0	1.0
M x F/S x E	M_{214}	0.0	0.0	0.0	2.0	0.0	1.0
Pooled error	M_{215}	0.0	0.0	0.0	0.0	0.0	1.0

D = dominance variance;

AE = additive genetic by environment interaction variance;

DE = dominance by environment interaction variance.

E_I = experimental error among plots in the Design I; and

E_{II} = experimental error among plots in the Design II.

The expectations of variances and covariances of metrical characters in genetical experiments could be expressed as shown by Mather (1949) as a sum of two genetic components (A measuring additive effects and D measuring dominance effects) and the appropriate environmental components E. If Y is the column vector of observed values (mean squares), X is the matrix of coefficients of the parameters to be estimated, B is the column vector of parameters to be estimated, and e is the column vector of random errors associated with each observation, then each of the equations in Table 15 can be represented by the model:

$$Y = XB + e \quad .$$

According to the Gauss-Markoff Theorem, given that:

$E(e) = \emptyset$ (null vector) and

$E(ee') = V(e) = V = \sigma_e^2.I$, where I is the identity matrix, in such model, then the method of least squares gives the Best Linear Unbiased Estimates (BLUES) for B. This means that by the least squares method, the estimate (which is the Normal Equation):

$$B = (X'X)^{-1} X'Y$$

gives a minimum variance with

$$V(B) = (X'X)^{-1}\sigma_e^2 \quad .$$

This method of estimation is correct only when the observed variances of mean squares are equal and covariances are uncorrelated. These conditions are seldom met in practical situations. Such restraints, as suggested by Mather (1949) could be overcome by a weighted least squares analysis. Silva (1974) in his intrapopulation components of variance studies, had good agreement between the weighted least squares estimates and the maximum likelihood estimates for the Design I and Design II combined. Hayman (1960) had indicated that the maximum likelihood method is simply an iterative weighted least squares method. In my study, the variances of the observed mean squares are not all equal; in other words, the matrix $V(e) \neq \sigma_e^2.I$ but is diagonal with unequal, diagonal elements. This means that the method of least squares will not give the best estimates. To correct for the unequal variances of mean squares, I used the transformation of the observations Y to other variables Z such that

$$Z = QB + f, \quad \text{where } E(f) = 0$$

$$V(f) = \sigma_e^2.I$$

and for F-tests to be valid, that $f \sim N(0, \sigma_e^2.I)$.
The transformation involves the use of weighted least squares analysis. The estimates obtained by this simpler method (as compared to maximum likelihood method) can then be expressed in terms of the original variable, Y. Transforming the original model $Y = XB + e$ by premultiplying it by the matrix

of weights, P^{-1}, gives:

$$P^{-1}Y = P^{-1}XB + P^{-1}e \quad .$$

The matrix of weights, P^{-1}, used is a diagonal matrix with the reciprocals of the standard errors of mean squares in the diagonal and zeros elsewhere. The form of the new weighted model makes the variance of each weighted mean square equal to unity. Writing $f = P^{-1}e$ so that $E(f) = 0$ and

$$E(ff') = V(f)$$

then

$$\begin{aligned} V(f) = E(ff') &= E(P^{-1}ee'P^{-1}) \\ &= P^{-1}E(ee')P^{-1} \\ &= P^{-1}PPP^{-1}\sigma_e^2 \quad , \text{ since } E(ee') = \text{var} - \text{cov}(e) \\ &\qquad\qquad\qquad\qquad\qquad\qquad = \sigma^2 \\ &= I\sigma_e^2 = I.I = I \quad . \end{aligned}$$

Using the weighted equations:

$$P^{-1}Y = P^{-1}XB + P^{-1}e \text{ or } Z = QB + f \quad .$$

The least squares method gives the following normal equations:

$$Q'QB = Q'Z \quad , \text{ which becomes}$$

$$X'V^{-1}XB = X'V^{-1}Y \quad , \text{ then } V = P'P = PP \quad .$$

The solution of the equations gives

$$B = (X'V^{-1}X)^{-1}X'V^{-1}Y$$

and $$\begin{aligned} V(B) &= (Q'Q)^{-1}\sigma_e^2 = (X'V^{-1}X)^{-1}\sigma_e^2 \\ &= (X'V^{-1}X)^{-1} \quad . \end{aligned}$$

Thus, the weights used are the standard errors of the mean squares obtained as $\sqrt{2(MS)^2/df + 2}$, where MS is the mean square and df is the respective degree of freedom. For the

weighting, the observed mean squares were divided by their respective standard errors. The normal least squares method was then used in the weighted equations to give the estimates with their respective standard errors. This procedure was done for each of the nine traits studied.

F. Correlations Among Interpopulation Traits

Additive genetic, dominance and phenotypic correlations were estimated for the n(n-1)/2 pairs of nine traits measured. A combined analysis of covariance for each pair of traits was used to obtain the respective components of covariation. From the pattern of mating in which males and females are randomly and independently sampled within each population and the experimental design in which their offspring are assigned to the replications at random, the expectations of mean products can be written in the form given by Mode and Robinson (1959), as shown in Tables 16 and 17. The additive genetic, dominance and phenotypic covariances are estimated from the expectations of mean products as done for the variances. Mode and Robinson (1959) have shown that the expectations of cross-products are the same as for mean squares. These covariance estimates, together with the variances, are then used for calculating the correlation coefficients.

The additive genetic, dominance, total genetic, and phenotypic correlations between the nine traits studied were calculated for the two mating schemes, Design I and Design II.

Table 16. Design I: Form of the analysis of covariance and expectation of mean products (E.M.P.) for a pair of traits (X and Y) pooled over sets in four environments

Source	d.f.	M.P.	E.M.P.[a]
Males (M)/sets (S)	s(m-1)	$M_{11}M_{11}'$	$\sigma_{XY} + 2\sigma_{f/mlXf/mlY} + 12\sigma_{mlXmlY} + 8\sigma_{f/mXf/mY} + 48\sigma_{mXmY}$
Females (F)/M/S	sm(f-1)	$M_{12}M_{12}'$	$\sigma_{XY} + 2\sigma_{f/mlXf/mlY} + 8\sigma_{f/mXf/mY}$
Males/S x Env. (E)	s(m-1)(l-1)	$M_{13}M_{13}'$	$\sigma_{XY} + 2\sigma_{f/mlXf/mlY} + 12\sigma_{mlXmlY}$
Females/M/S/ x E	sm(f-1)(l-1)	$M_{14}M_{14}'$	$\sigma_{XY} + 2\sigma_{f/mlXf/mlY}$
Pooled error	sl(mf-1)(r-1)	$M_{15}M_{15}'$	σ_{XY}

[a]Expectation of mean product, where σ_{XY} is the error covariance for traits X and Y; $\sigma_{f/mlXf/mlY}$ is the covariance due to genotype x environment interactions for females within males between traits X and Y; σ_{mlXmlY} is the covariance due to genotype x environment interactions for males between traits X and Y; $\sigma_{f/mSf/mY}$ is the covariance of female effects between traits X and Y; and σ_{mXmY} is the covariance of male effects between traits X and Y.

Table 17. Design II: Form of the analysis of covariance and expectation of mean products (E.M.P.) for a pair of traits (X and Y) pooled over sets in four environments

Source	d.f.	M.P.	E.M.P.[a]
Males (M)/sets (S)	s(m-1)	$M_{21}M_{21}'$	$\sigma_{XY} + 2\sigma_{mflXmflY} + 8\sigma_{fmXmfY} + 8\sigma_{mlXmlY} + 32\sigma_{mXmY}$
Females (F)/S	**s(f-1)**	$M_{22}M_{22}'$	$\sigma_{XY} + 2\sigma_{mflXmflY} + 8\sigma_{mfXmfY} + 8\sigma_{flXflY} + 32\sigma_{fXfY}$
M x F/S	s(m-1)(f-1)	$M_{23}M_{23}'$	$\sigma_{XY} + 2\sigma_{mflXmflY} + 8\sigma_{mfXmfY}$
M/S x env. **(E)**	s(m-1)(l-1)	$M_{24}M_{24}'$	$\sigma_{XY} + 2\sigma_{mflXmflY} + 8\sigma_{mlXmlY}$
F/S x E	s(f-1)(l-1)	$M_{25}M_{25}'$	$\sigma_{XY} + 2\sigma_{mflXmflY} + 8\sigma_{flXflY}$
M x F/S x E	s(m-1)(f-1)(l-1)	$M_{26}M_{26}'$	$\sigma_{XY} + 2\sigma_{mflXmflY}$
Pooled error	sl(mf-1)(r-1)	$M_{27}M_{27}'$	σ_{XY}

[a] $\sigma_{mflXmflY}$ is the three-way interaction covariance between males, females and the environment between traits X and Y.

In section IV C, it was shown that, in the Design I (assuming no epistasis and F = 0), $(\sigma^2_{m_{12}} + \sigma^2_{m_{21}}) = \frac{1}{2}\sigma^2_{A_{(12)}}$; $\sigma^2_m = \frac{1}{4}\sigma^2_A$; $\sigma^2_{f/m} = \frac{1}{4}\sigma^2_A + \frac{1}{4}\sigma^2_D$ and $4\sigma^2_{f/m} = \sigma^2_G$. Similarly, in Design II (F = 1), $2\sigma^2_m = 2\sigma^2_f = \sigma^2_A$, $\sigma^2_{mf} = \sigma^2_D$, and $\sigma^2_m + \sigma^2_f + \sigma^2_{mf} = \sigma^2_G$. By definition then, the correlation coefficients were computed as follows for Design I:

$$r_A = \frac{\sigma_{mXY}}{\sqrt{\sigma^2_{mX} \cdot \sigma^2_{mY}}} = \text{additive genetic correlation,}$$

where

σ_{mXY} = male component of genetic covariance between traits X and Y;

σ^2_{mX} = male component of genetic variation for trait X; and

σ^2_{mY} = male component of genetic variation for trait Y.

$$r_D = \frac{\sigma_{f/mXY} - \sigma_{mXY}}{\sqrt{(\sigma^2_{f/mX} - \sigma^2_{mX})(\sigma^2_{f/mY} - \sigma^2_{mY})}} = \text{dominance correlation,}$$

where

$\sigma_{f/mXY}$ = female within male component of genetic covariance between traits X and Y; and

$\sigma^2_{f/mX}, \sigma^2_{f/mY}$ = female within male component of genetic variation for trait X and trait Y, respectively.

$$r_G = \frac{\sigma_{f/mXY}}{\sqrt{\sigma^2_{f/mX} \cdot \sigma^2_{f/mY}}} = \text{total genetic correlation,}$$

and

$$r_P = \frac{4\sigma_{f/mXY} + \sigma_{XY}}{\sqrt{(4\sigma^2_{f/mX}+\sigma^2_X)(4\sigma^2_{f/mY}+\sigma^2_Y)}} = \text{phenotypic correlation,}$$

where

σ_{XY} = error covariance for traits X and Y, and

σ^2_X, σ^2_Y = error variance for trait X and trait Y, respectively.

In the same way, correlation coefficients were computed for Design II, as follows:

$$r_A = \frac{\sigma_{mXY} + \sigma_{fXY}}{\sqrt{(\sigma^2_{mX}+\sigma^2_{fX})(\sigma^2_{mY}+\sigma^2_{fY})}} ,$$

where

σ_{fXY} = female component of genetic covariation for traits X and Y; and

$\sigma^2_{fX}, \sigma^2_{fY}$ = female component of genetic variation for trait X and trait Y, respectively.

$$r_D = \frac{\sigma_{mfXY}}{\sqrt{\sigma^2_{fmX} \cdot \sigma^2_{mfY}}} ,$$

where

σ_{mfXY} = male x female interaction covariance for traits X and Y; and

$\sigma^2_{mfX}, \sigma^2_{mfY}$ = male x female interaction variance for trait X and trait Y, respectively.

$$r_G = \frac{\sigma_{mXY} + \sigma_{fXY} + \sigma_{mfXY}}{\sqrt{(\sigma^2_{mX}+\sigma^2_{fX}+\sigma^2_{mfX})(\sigma^2_{mY}+\sigma^2_{fY}+\sigma^2_{mfY})}} ,$$

and

$$r_P = \frac{\sigma_{mXY} + \sigma_{fXY} + \sigma_{mfXY} + \sigma_{XY}}{\sqrt{(\sigma^2_{mX}+\sigma^2_{fX}+\sigma^2_{mfX}+\sigma^2_{X})(\sigma^2_{mY}+\sigma^2_{fY}+\sigma^2_{mfY}+\sigma^2_{Y})}} .$$

In obtaining estimates of correlation coefficients for the combined Designs I and II, the mean products are also used. Using the same genetic model and matrix notation as for the combined DI and II variance estimates (Table 15), the mean products are converted into genetic, environmental and genetic by environmental covariances in the form shown in Table 18. A weighted least squares analysis (as used with the mean squares for the combined variance estimates) was used to solve the equations generated, in order to obtain the estimates of genetic, environmental and genetic by environmental covariances. The weights used were reciprocals of the standard errors of the mean products which is shown as:

$$\sqrt{\frac{[(MS_1)(MS_2) + (MP_{12})^2]}{(df + 2)}} ,$$

where

MS_1 = mean square for trait 1,

MS_2 = mean square for trait 2,

MP_{12} = mean product for traits 1 and 2, and

df = degrees of freedom for the mean product.

Table 18. Matrix of mean products for two groups of 10 sets (DI) and one group of 20 sets (DII) pooled over sets and combined over four environments. Translation is in terms of genetic, environmental, and genetic x environmental covariances for a pair of traits[a]

	M.P.	AA'	DD'	AEA'E'	DED'E'	EE_I'	EE_{II}'
			Design I				
			(BS10♀ x BS11♂)				
Males (M)/sets (X)	$M_{11}M_{11}'$	14.0	2.0	3.5	0.5	1.0	0.0
Females (F)/M/S	$M_{12}M_{12}'$	2.0	2.0	0.5	0.5	1.0	0.0
Males/S x environments (E)	$M_{13}M_{13}'$	0.0	0.0	3.5	0.5	1.0	0.0
Females/M/S x E	$M_{14}M_{14}'$	0.0	0.0	0.5	0.5	1.0	0.0
Pooled error	$M_{15}M_{15}'$	0.0	0.0	0.0	0.0	1.0	0.0
			(BS10♂ x BS11♀)				
Males (M)/sets (X)	$M_{11}M_{11}'$	14.0	2.0	3.5	0.5	1.0	0.0
Females (F)/M/S	$M_{12}M_{12}'$	2.0	2.0	0.5	0.5	1.0	0.0
Males/S x environments (E)	$M_{13}M_{13}'$	0.0	0.0	3.5	0.5	1.0	0.0
Females/M/S x E	$M_{14}M_{14}'$	0.0	0.0	0.5	0.5	1.0	0.0
Pooled error	$M_{15}M_{15}'$	0.0	0.0	0.0	0.0	1.0	0.0

[a] AA' = additive genetic covariance; DD' = dominance covariance; and AEA'E' = additive x environmental interaction variance; DED'E' = dominance x environmental interaction covariance; EE_I' = environmental covariance for Design I; EE_{II}' = environmental covariance for Design II.

Table 18. (Continued)

	M.P.	AA'	DD'	AEA'E'	DED'E'	EE_I'	EE_{II}'
		Design II					
Males (M)/sets (S)	$M_{21}M_{21}$'	16.0	8.0	4.0	2.0	0.0	1.0
Females (F)/S	$M_{22}M_{22}$'	16.0	8.0	4.0	2.0	0.0	1.0
M x F/S	$M_{23}M_{23}$'	0.0	8.0	0.0	2.0	0.0	1.0
M/S x E	$M_{24}M_{24}$'	0.0	0.0	4.0	2.0	0.0	1.0
F/S x E	$M_{25}M_{25}$'	0.0	0.0	4.0	2.0	0.0	1.0
M x F/S x E	$M_{26}M_{26}$'	0.0	0.0	0.0	2.0	0.0	1.0
Pooled error	$M_{27}M_{27}$'	0.0	0.0	0.0	0.0	0.0	1.0

The standard error estimates thus obtained are unbiased. For the weighting, the mean products were divided by their respective standard errors, before the least squares method was applied to solve the resulting weighted equations.

The correlations were calculated using the following relationships:

$$r_A = \frac{AA'}{\sqrt{(A)(A')}} = \text{additive genetic correlation,}$$

where A is the additive genetic variance for trait X;

A' is the additive genetic variance for trait Y; and

AA' is the additive genetic covariance among the traits X and Y.

$$r_D = \frac{DD'}{\sqrt{(D)(D')}} = \text{dominance correlation,}$$

where D is the dominance variance for trait X;

D' is the dominance variance for trait Y; and

DD' is the dominance covariance among the traits X and Y.

$$r_G = \frac{GG'}{\sqrt{(G)(G')}} = \text{total genetic correlation,}$$

where G is the genetic variance for trait X = A + D;

G' is the genetic variance for trait Y = A' + D';

GG' is the genetic covariance among the traits X and Y = AA' + DD' .

$$r_E = \frac{EE'}{\sqrt{(E)(E')}} = \text{error correlation,}$$

where E is the error variance for trait X;

E' is the error variance for trait Y; and

EE' is the error covariance among the traits X and Y.

$$r_P = \frac{PP'}{\sqrt{(P)(P')}} = \text{phenotypic correlation,}$$

where P is the phenotypic variance for trait X = G + E + GE;

P' is the phenotypic variance for trait Y = G' + E' + G'E'; and

PP' is the phenotypic covariance for traits X and Y = GG' + EE' + GE G'E', where

GE is the genotype by environment interaction variance for trait X = (AE) + (DE);

G'E' is the genotype by environment interaction variance for trait Y = (A'E') + (D'E'); and

GE,G'E' is the genotype by environment interaction covariance for traits X and Y = (AA' x EE') + (DD' x EE').

G. Expected Genetic Progress from Reciprocal Full-sib Selection (RFS)

Basically, reciprocal full-sib selection is an inter-population recurrent selection scheme that evaluates and selects full-sib progenies generated from crossing two populations. The expected gain from selection, therefore, refers to the improvement of the population cross. The expected genetic change from selection for yield and other traits could be predicted from the general formula:

and 1 is the number of environments. The parental control, c, is unity (one) and is not shown in the formula.

The expected progress from selection was computed using Design I (DI) estimates, Design II (DII) estimates, and DI and DII estimates combined.

V. RESULTS

A. Analysis of Variance

General means and standard errors of the means for the nine traits measured for 480 Design I (DI) and 320 Design II (DII) full-sib progenies in the variety cross, BS10 x BS11, are presented in Table 19. All of the traits, with the exception of days to silk emergence, were measured in four environments (Ames - 1973, 1974, and 1975; and Ankeny - 1973). Days to silk were measured in three environments (1973, 1974, and 1975 in Ames). Table 19 also shows the coefficient of variability (C.V.) for the traits. Except for the very high C.V.'s for tiller number and tiller height, the C.V.'s were acceptable. The C.V.'s range from 3.98% for ear diameter to 11.59% for grain yield. The relatively high C.V.'s recorded for tiller number and tiller height (73.83% and 66.38%, respectively) could be due to the high experimental errors associated with the traits, irrespective of the size of the trait means.

To obtain a valid comparison between the DI and DII means, a t-test of the difference ($\bar{d}$) between the full-sib means was computed. The formula used in this case was:

$$t = \frac{\bar{d}}{s_{\bar{d}}}, \text{ where } \bar{d} = \bar{X}_{FSI} - \bar{X}_{FSII} \text{ or vice versa}$$

$\bar{X}_{FSII} - \bar{X}_{FSI}$; and

Table 19. General means and coefficient of variation for nine traits measured for the interpopulation (BS10 x BS11) in the Design I and Design II experiments

Trait	Design I	Design II
Silk (days)[a]	23.54 ± 0.28 (7.62)[b]	24.53 ± 0.22 (4.55)
Ear height (cm)	117.08 ± 1.06 (8.89)	122.80 ± 0.91 (5.49)
Tiller number	4.07 ± 0.36 (73.83)	5.04 ± 0.34 (47.82)
Tiller height (cm)	96.50 ± 7.76 (66.38)	98.07 ± 7.45 (60.75)
Ear length (cm)	19.01 ± 0.17 (7.38)	18.71 ± 0.14 (5.66)
Ear diameter (cm)	4.63 ± 0.03 (4.70)	4.51 ± 0.03 (3.98)
Cob diameter (cm)	2.78 ± 0.02 (5.62)	2.67 ± 0.02 (4.88)
Kernel depth (cm)	1.85 ± 0.02 (9.71)	1.81 ± 0.02 (9.25)
Yield (g/plant)	200.35 ± 2.88 (11.59)	200.98 ± 3.10 (11.41)

[a]Days from July 1 to 50% silk emergence.

[b]Numbers in parentheses are coefficient of variation in percent (C.V., %).

$$s_{\bar{d}} = \sqrt{\frac{\sigma_I^2}{r_I} + \frac{\sigma_{II}^2}{r_{II}}} \quad .$$

σ_I^2 and σ_{II}^2 are respective error mean squares in DI and DII; and

r_I and r_{II} are number of entries (480 and 320), respectively) from which the means were obtained.

The degrees of freedom for the test were those for the error mean squares. The t-tests showed that the means for days to silk emergence, ear height, and tiller number in DI full-sibs, were significantly different (5% and 1% probability levels) from those obtained in the DII full-sib progenies. The observed differences (Table 19) in these three traits were, however, very small. There were no significant differences between the full-sib progenies of Design I and the full-sib progenies of Design II in the variety cross (interpopulation) for each of the other six traits measured. Most of the traits, including Yield (200.35 g/plant and 200.98 g/plant for DI and DII, respectively) show striking similarities. A definite trend, however, was shown by the estimates of standard error (SE) and coefficient of variability. For all the traits, the C.V. was lower for the DII than the DI. Days to silk, ear height, tiller number, tiller height, and ear length have lower SE estimates for DII than DI, while for ear diameter, cob diameter, and kernel depth, the SE estimates are the same. Yield had a slightly higher SE in DII than DI.

An analysis of variance for all the 20 sets combined across the four environments was computed for each of the traits. The combined analysis of variance in the DI and DII, together with the results of the F-tests for the deviation of the mean squares from zero, are presented in Tables 20 and 21. Highly significant differences (1% probability level) were observed among the males and females in DI and DII for all the traits measured. The significant F-tests confirm the presence of genetic variability for all the traits in the interpopulation. Significant interactions (5% and 1% probability levels) among the males and females in both mating designs with environments were indicated for all traits except days to silk, ear diameter, and cob diameter in DI. Only the male interaction with the environment (significant at 1% level) was, however, indicated for ear length and kernel depth in DI. This observation also confirms the presence of genetic by environment interaction variability for all the traits studied, as indicated also in the DII analyses. Significant interactions (1% level) also were recorded for the interaction of males and females in DII (confirming presence of dominance type of genetic variability for the assumption of no epistasis) for all nine traits. The interaction between males and females with environment also was shown to be significant for all traits, except cob diameter. For a more sensitive F-test, the analysis of variance was pooled over the 20 sets and four environments for the DI and DII. The pooled analysis of

Table 20. Combined analysis of variance for 20 sets across four environments for ear height, tiller number and tiller height and three environments for days to silk in Design I and Design II

Source	DF[a]	Mean squares: Days to silk	Ear height	Tiller number	Tiller height	DF[b]
		Design I				
Male (M)/set (S)	60	39.14**	3135.94**	145.49**	25333.01**	60
Female (F)/M/S	400	8.57**	471.36**	34.29**	7747.34**	400
Environment (E) x M/S	120	3.33	119.05**	16.31**	4523.33**	180
E x F/M/S	800	2.52	71.69**	8.26**	3856.74**	1200
Pooled error	1380	2.79	60.22	6.41	3485.65	1840
		Design II				
Male (M)/set (S)	60	35.20**	1930.48**	206.68**	27634.90**	60
Female (F)/S	60	36.78**	2565.27**	260.49**	33140.32**	60
(M x F)/S	180	4.25**	189.70**	20.16**	6343.96**	180
Environment (E) x M/S	120	2.86**	98.02**	19.55**	5083.04**	180
Environment (E) x F/S	120	2.09*	132.85**	17.08**	4501.16**	180
E x (M x F)/S	360	1.69**	53.02**	7.34**	3558.29**	540
Pooled error	900	1.24	45.47	5.81	3549.86	1200

[a]DF = degree of freedom; days to silk were recorded in three environments.

[b]DF for traits measured in four environments.

*,**Significant at the 5% and 1% levels of probability, respectively, in this table and the following tables.

Table 21. Combined analysis of variance for 20 sets across four environments for five traits in Design I and Design II

Source	DF	Mean squares: Ear length x10^2	Ear diameter x10^2	Cob diameter x10^2	Kernel depth x10^2	Yield
		Design I				
Male (M)/set (S)	60	2578.49**	63.04**	27.54**	34.02**	3789.10**
Female (F)/M/S	400	533.67**	13.58**	7.76**	6.25**	1075.42**
Environment (E) x M/S	180	199.76**	5.15	2.32	3.59**	1112.21**
E x F/M/S	1200	163.69	3.58	1.69	2.89	539.54**
Pooled error	1840	176.64	5.39	2.46	3.06	465.49
		Design II				
Male (M)/set (S)	60	2676.26**	58.62**	22.47**	37.89**	2723.32**
Female (F)/S	60	3025.22**	75.28**	28.69**	44.99**	5493.26**
(M x F)/S	180	350.52**	6.61**	3.09**	4.40**	1152.87**
Environment (E) x M/S	180	197.09**	6.11**	2.66**	4.97**	1194.51**
Environment (E) x F/S	180	294.91**	5.60**	3.06**	4.57**	1261.67**
E x (M x F)/S	540	132.51**	4.25**	1.67	3.64**	616.69**
Pooled error	1200	112.12	3.22	1.74	2.80	525.66

variance for yield is shown in Table 22. Significant tests (1% level) were shown for the males and females in both designs and for the male by female interaction in DII. However, the significant interactions with environments in the sources of variation indicated in the combined analysis (Tables 20 and 21) nullify the validity of the F-tests in the pooled analysis.

B. Estimates of Interpopulation Genetic Variances

For the estimation of the components of genetic variance, error variance, and their interactions, I used the simple genetic model that includes only the additive (σ^2_A) and dominance (σ^2_D) portions of the genetic variation and the interaction of these (σ^2_{AE} and σ^2_{DE}) with the environments, and the experimental error (σ^2). I have assumed the absence of epistatic effects. Since the estimates of the variance components are linear functions of mean squares, the variance of such estimates can be described as a function of the variances of the mean squares contributing to the estimates. Consequently, all mean squares that showed significant differences from zero should give significant estimates of the genetic variance components.

In this study, I have three estimates for each of the five variance components reported. Three estimates were derived from each of the two mating designs, DI and DII, and a combination of the two designs, DI,II. For DI, the estimates were obtained in two ways, as described in section IV C. First,

Table 22. Analysis of variance pooled over 20 sets in four experiments for yield in Design I and Design II

Design I			Design II		
Source	DF	Mean squares	Source	DF	Mean squares
Environments (E)	3	156090.75**	E	3	67963.27**
Sets (S)	19	3597.16**	S	19	9457.57**
S/E	57	3057.90**	S/E	57	4635.64**
Replications (R)/S/E	80	610.81	R/S/E	80	1398.15**
Males (M)/S/E	240	4901.31**	M/S/E	240	1826.71**
Females (F)/M/S/E	1600	1605.97**	F/S/E	240	2319.57**
Pooled error	1840	996.03	M x F/S/E	720	750.73**
			Pooled error	1200	525.66

variance components were estimated for the two groups of progenies, 12 and 21, for all traits. The interpopulation variance components were then calculated as $\frac{1}{2}(12) = \frac{1}{2}(12 + 21)$. Second, the interpopulation estimates were obtained directly from the analysis of the data for all progenies together. Table 23 shows the estimates of genetic and error variance components with their standard errors for nine traits for the two groups of progenies, 12 and 21, in Design I. Except for tiller number, the two estimates of σ^2_A ($\sigma^2_{A_{12}}$ and $\sigma^2_{A_{21}}$) show no significant differences for all traits, as well as the estimates of σ^2_{AE} ($\sigma^2_{AE_{12}}$ and $\sigma^2_{AE_{21}}$). There are no significant differences between the two estimates of σ^2_D ($\sigma^2_{D_{12}}$ and $\sigma^2_{D_{21}}$) for the five traits, days to silk, ear height, ear length, ear diameter, and yield. However, for tiller number, tiller height, and two yield components, cob diameter and kernel depth, significant differences were shown between the two σ^2_D estimates. Some of these estimates of σ^2_D are either negative or nonsignificantly different from zero. Most of the two estimates of σ^2_{DE} for the traits, except ear height and tiller number, show significant differences. Significant differences were detected for the two estimates of σ^2 for all traits except tiller height, ear length, and yield. The occurrence of significant differences between the two estimates of variance components shown in Table 23, is an indication of the presence of reciprocal or maternal effects for the relevant traits. In terms of the additive genetic variance (σ^2_A) therefore, there

Variance component estimates		
σ^2_{AE}	σ^2_{DE}	σ^2
0.20 ± 0.14	-1.83 ± 0.09	2.47 ± 0.13
0.34 ± 0.28	0.20 ± 0.17	3.10 ± 0.17
NS	S	S
21.93 ± 6.87	-17.52 ± 4.97	68.97 ± 3.21
9.64 ± 5.16	-31.83 ± 3.79	51.46 ± 2.40
NS	NS	S
3.66 ± 1.04	0.40 ± 0.75	7.87 ± 0.37
1.70 ± 0.59	1.63 ± 0.43	4.96 ± 0.23
NS	NS	S
408.43 ± 259.22	-40.17 ± 192.94	3647.79 ± 744.52
35.97 ± 209.78	1080.16 ± 160.07	3323.51 ± 154.79
NS	S	NS
23.79 ± 11.38	-97.22 ± 8.48	189.00 ± 8.80
0.26 ± 9.27	21.37 ± 7.14	164.27 ± 7.65
NS	S	NS
0.63 ± 0.30	-6.67 ± 0.23	7.05 ± 0.33
0.42 ± 0.22	1.60 ± 0.17	3.72 ± 0.17
NS	S	S
0.24 ± 0.13	-2.60 ± 0.10	2.95 ± 0.14
0.18 ± 0.11	0.92 ± 0.08	1.98 ± 0.09
NS	S	S
0.29 ± 0.21	-0.76 ± 0.16	3.41 ± 0.16
0.18 ± 0.16	0.37 ± 0.12	2.70 ± 0.13
NS	S	S
213.26 ± 58.35	-152.53 ± 41.86	498.50 ± 23.22
174.52 ± 52.89	24.97 ± 38.05	432.48 ± 20.14
NS	S	NS

are no reciprocal or maternal effects shown by all the traits studied, except tiller number. Grain yield from the comparison of the two estimates of the variance components shows no reciprocal or maternal effects. Estimates obtained for the variance components when all DI progenies were analyzed together, and not identifying crosses or reciprocal crosses, were half the magnitude of estimates obtained from the two groups of progenies (Table 24) using the relationship $\frac{1}{2}(\sigma^2_{A_{12}} + \sigma^2_{A_{21}}) = \frac{1}{2}\sigma^2_{A_{(12)}}$ (DI').

The three estimates of interpopulation genetic and error variance components with their standard errors and the ratio of dominance variance to additive genetic variance for nine traits are presented in Tables 25 and 26. The estimates of additive genetic variance, $\sigma^2_{A_{1(12)}}$ (DI), $\sigma^2_{A_{2(12)}}$ (DII) and $\sigma^2_{A_{(12)}}$ (DI,II) were significant and positive for all traits. For DI, the estimates of $\sigma^2_{A_{1(12)}}$ were greater than twice their standard errors for all the traits. Also, the estimates of $\sigma^2_{A_{2(12)}}$ for DII were greater than twice the values of their standard errors for all traits. All the estimates of additive genetic variance in both designs were actually greater than three times the magnitude of their respective standard error. In the combined DI,II, except for tiller height and yield, all other traits had estimates of $\sigma^2_{A_{(12)}}$, greater than twice the standard errors. In this design combination, although $\sigma^2_{A_{(12)}}$ estimates for tiller height and yield were greater than their standard errors, they were not twice as large as in the

Variance component estimates		
$\sigma^2_{AE_{(12)}}$	$\sigma^2_{DE_{(12)}}$	$\sigma^2_{(12)}$
0.27 ± 0.15	-0.07 ± 0.13	2.79 ± 0.11
0.54 ± 0.42	-1.64 ± 0.26	5.58 ± 0.30
15.79 ± 4.27	7.15 ± 4.39	60.22 ± 1.98
31.58 ± 12.04	49.36 ± 9.36	120.44 ± 5.62
2.68 ± 0.58	1.02 ± 0.59	6.41 ± 0.21
5.36 ± 1.64	2.04 ± 1.18	12.84 ± 0.60
222.20 ± 166.53	519.99 ± 177.07	3485.65 ± 114.86
444.40 ± 469.00	1040.00 ± 353.02	6971.30 ± 899.32
12.02 ± 7.33	-37.93 ± 7.83	176.64 ± 5.82
24.04 ± 20.66	-75.86 ± 15.62	353.28 ± 16.46
0.52 ± 0.19	-4.14 ± 0.20	5.39 ± 0.18
1.06 ± 0.52	-5.08 ± 15.62	10.78 ± 0.50
0.21 ± 0.08	-1.76 ± 0.09	2.46 ± 0.08
0.42 ± 0.24	-1.68 ± 0.18	4.94 ± 0.24
0.23 ± 0.13	-0.57 ± 0.14	3.06 ± 0.10
0.48 ± 0.38	-2.00 ± 0.28	6.12 ± 0.30
193.89 ± 39.53	-63.78 ± 40.16	465.49 ± 15.34
387.78 ± 111.22	-127.56 ± 79.92	930.98 ± 43.36

Variance component estimates			$\sigma^2_{D_{(12)}}$ [a]
$\sigma^2_{AE_{(12)}}$	$\sigma^2_{DE_{(12)}}$	$\sigma^2_{(12)}$	$\sigma^2_{A_{(12)}}$
0.27 ± 0.15	-0.07 ± 0.13	2.79 ± 0.11	22
0.20 ± 0.04	0.22 ± 0.07	1.24 ± 0.06	17
-0.01 ± 0.19	0.54 ± 0.33	3.71 ± 0.33[b]	0
		0.92 ± 0.10[b]	
15.79 ± 4.27	7.15 ± 4.39	60.22 ± 1.98	0
15.60 ± 1.58	3.78 ± 1.84	45.47 ± 1.77	14
-16.42 ± 26.91	63.66 ± 49.74	222.47 ± 23.39[b]	0
		-25.87 ± 3.01[b]	
2.68 ± 0.58	1.02 ± 0.59	6.41 ± 0.21	51
2.75 ± 0.25	0.76 ± 0.25	5.81 ± 0.23	13
4.03 ± 1.72	-1.73 ± 3.18	-0.38 ± 0.00[b]	54
		9.03 ± 1.02[b]	
222.20 ± 166.53	519.99 ± 177.07	3485.65 ± 114.86	4
308.45 ± 68.41	421.00 ± 128.24	3549.86 ± 138.07	24
256.04 ± 287.36	111.42 ± 447.18	3656.06 ± 268.80[b]	26
		3461.92 ± 328.10[b]	

Variance component estimates			$\frac{\sigma^2_{D(12)}}{\sigma^2_{A(12)}}$ [a]
$\sigma^2_{AE(12)}$	$\sigma^2_{DE(12)}$	$\sigma^2_{(12)}$	
12.02 ± 7.33	-37.93 ± 7.83	176.64 ± 5.82	11
28.37 ± 3.43	10.20 ± 4.58	112.12 ± 4.36	18
14.00 ± 22.84	24.52 ± 40.14	173.27 ± 15.86[b]	9
		113.28 ± 12.27[b]	
0.52 ± 0.19	-4.14 ± 0.20	5.39 ± 0.18	25
0.40 ± 0.08	0.51 ± 0.14	3.22 ± 0.13	8
0.10 ± 0.04	0.73 ± 0.74	5.14 ± 0.46[b]	0
		3.21 ± 0.35[b]	
0.21 ± 0.08	-1.76 ± 0.09	2.46 ± 0.08	90
0.30 ± 0.04	-0.03 ± 0.06	1.74 ± 0.07	13
-0.08 ± 0.16	0.46 ± 0.24	3.28 ± 0.28[b]	0
		1.37 ± 0.14[b]	
0.23 ± 0.13	-0.57 ± 0.14	3.06 ± 0.10	0
0.28 ± 0.07	0.42 ± 0.12	2.80 ± 0.11	4
0.32 ± 0.30	0.22 ± 0.51	2.23 ± 0.20[b]	6
		3.18 ± 0.11[b]	
193.89 ± 39.53	-63.78 ± 40.16	465.49 ± 15.34	53
152.85 ± 16.75	45.51 ± 21.58	525.66 ± 21.44	38
168.27 ± 39.61	27.65 ± 54.33	483.16 ± 34.51[b]	37
		515.62 ± 45.30[b]	

individual designs.

Some of the three estimates of dominance variance ($\sigma^2_{D_{(12)}}$) computed by the three procedures were negative. In DI, negative estimates were obtained for ear height and kernel depth; the remaining traits, days to silk, tiller number, tiller height, ear length, ear diameter, cob diameter and yield, had positive estimates. All estimates of DII were positive. Negative estimates of dominance were obtained in DI,II, for days to silk, ear height, ear diameter, and cob diameter. All the $\sigma^2_{D_{(12)}}$ estimates in DI,II, whether positive or negative, were associated with relatively large standard errors; hence, all estimates were not different from zero. Kernel depth shows estimates of $\sigma^2_{D_{(12)}}$ that are not significantly different from zero for all three estimation procedures.

The three estimates of the interaction of the genetic variances with environment were significant and positive in most instances. The additive x environment interaction variance ($\sigma^2_{AE_{(12)}}$) estimates were positive for all traits in the DI, DII, and DI,II except for days to silk, ear height, and cob diameter in DI,II. More negative estimates were obtained for the dominance x environment interaction variance ($\sigma^2_{DE_{(12)}}$). In DI, $\sigma^2_{DE_{(12)}}$ estimates for days to silk, all of the yield components (ear length, ear diameter, cob diameter, and kernel depth), and yield, were negative. In DII and DI,II, estimates of $\sigma^2_{DE_{(12)}}$ were negative only for cob diameter and tiller number, respectively.

the three designs for all traits. There was, also, no regular trend in the three values from trait to trait. Zero values are shown for the traits which have negative estimates of $\sigma^2_{D(12)}$.

C. Interpopulation Correlations

In Design I (DI) and Design II (DII), the mean squares and mean products from the combined analyses of variance and covariance were used in computing the design components of variance and covariance. The design components are used to compute the correlation coefficients among all the traits studied, as shown in section IV F. In the combined DI and DII, from the mean squares and mean products, the genetic variances and covariances among traits were estimated using weighted least squares to solve the 17 equations generated in the matrices of mean squares and mean products. By use of the procedures described in section IV F, with the variance estimates obtained for every trait and the estimates of covariances among pairs of traits, several types of correlation coefficients were computed. The correlation coefficients of additive genetic correlation (r_A), dominance correlations (r_D), genotypic correlations (r_G), phenotypic correlations (r_P), and error correlations (r_e) among all traits are presented in Tables 27 to 40.

For the additive genetic correlations (r_A), highest coefficients were obtained between tiller height and tiller

Table 27. Additive genetic correlation coefficients (r_A) among nine traits for the interpopulation (BS10 x BS11) in Design I

Trait	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.36							
Tiller number	-0.21	-0.25						
Tiller height	0.00	-0.25	0.95					
Ear length	0.16	0.07	-0.08	0.05				
Ear diameter	0.26	0.44	0.04	0.01	-0.33			
Cob diameter	0.32	0.37	0.00	-0.10	0.12	0.68		
Kernel depth	0.12	0.28	0.02	0.07	-0.53	0.80	0.10	
Yield	0.33	0.79	-0.21	-0.04	0.22	0.47	0.23	0.44

Table 28. Dominance correlation coefficients (r_D) among nine traits for the interpopulation (BS10 x BS11) in Design I

Trait	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.31							
Tiller number	0.04	0.03						
Tiller height	0.02	0.16	0.74					
Ear length	0.16	0.09	-0.03	-0.10				
Ear diameter	0.11	0.11	-0.23	-0.44	-0.07			
Cob diameter	0.10	-0.02	-0.21	-0.36	0.23	0.81		
Kernel depth	0.05	0.21	-0.09	-0.21	-0.43	0.62	0.04	
Yield	0.25	0.61	0.10	0.20	0.37	0.24	0.11	0.27

Table 29. Genotypic correlation coefficients (r_G) among nine traits for the inter-population (BS10 x BS11) in Design I

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.32							
Tiller number	-0.02	-0.05						
Tiller height	0.02	0.03	0.79					
Ear length	0.16	0.08	-0.05	-0.06				
Ear diameter	0.15	0.21	-0.16	-0.31	-0.15			
Cob diameter	0.15	0.09	-0.16	-0.30	0.20	0.78		
Kernel depth	0.07	0.24	-0.05	-0.12	-0.46	0.67	0.06	
Yield	0.27	0.66	0.02	0.14	0.33	0.30	0.14	0.32

Table 30. Phenotypic correlation coefficients (r_p) among nine traits for the inter-population (BS10 x BS11) in Design I

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.26							
Tiller number	0.02	-0.03						
Tiller height	0.04	0.02	0.41					
Ear length	0.15	0.10	0.00	0.02				
Ear diameter	0.21	0.19	-0.07	-0.09	0.25			
Cob diameter	0.22	0.12	-0.08	-0.09	0.35	0.71		
Kernel depth	0.09	0.15	-0.02	-0.03	0.01	0.69	0.02	
Yield	0.12	0.37	0.06	0.13	0.45	0.43	0.26	0.34

Table 31. Error correlation coefficients (r_e) among nine traits for the inter-population (BS10 x BS11) in Design I

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.21							
Tiller number	0.06	0.01						
Tiller height	0.05	0.02	0.17					
Ear length	0.15	0.13	0.05	0.06				
Ear diameter	0.26	0.18	0.01	0.02	0.52			
Cob diameter	0.27	0.18	0.01	0.02	0.46	0.67		
Kernel depth	0.10	0.08	0.01	0.01	0.29	0.71	0.00	
Yield	0.04	0.18	0.09	0.13	0.53	0.50	0.34	0.35

Table 32. Additive genetic correlation coefficients (r_A) among nine traits for the interpopulation (BS10 x BS11) in Design II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.32							
Tiller number	0.17	-0.06						
Tiller height	0.04	-0.08	0.93					
Ear length	0.04	-0.05	-0.12	-0.25				
Ear diameter	-0.04	0.03	0.05	0.01	-0.22			
Cob diameter	-0.14	-0.26	-0.02	-0.01	0.05	0.59		
Kernel depth	0.03	0.21	0.06	0.01	-0.32	0.80	-0.02	
Yield	0.16	0.53	-0.06	0.04	0.16	0.33	0.04	0.35

Table 33. Dominance correlation coefficients (r_D) among nine traits for the inter-population (BS10 x BS11) in Design II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.19							
Tiller number	0.16	-0.11						
Tiller height	0.02	-0.06	0.31					
Ear length	-0.08	-0.20	-0.11	-0.11				
Ear diameter	-0.09	0.27	0.16	0.17	-0.14			
Cob diameter	0.02	0.30	0.02	0.07	-0.20	0.86		
Kernel depth	-0.12	0.10	0.32	0.20	0.07	0.74	0.29	
Yield	-0.05	0.41	0.17	0.02	0.21	0.20	0.49	-0.21

Table 34. Genotypic correlation coefficients (r_G) among nine traits for the inter-population (BS10 x BS11) in Design II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.30							
Tiller number	0.17	-0.07						
Tiller height	0.04	-0.08	0.83					
Ear length	0.02	-0.07	-0.12	-0.22				
Ear diameter	-0.05	0.05	0.06	0.03	-0.20			
Cob diameter	-0.12	-0.19	-0.01	0.01	0.01	0.61		
Kernel depth	0.02	0.20	0.07	0.03	-0.28	0.79	0.00	
Yield	0.12	0.50	-0.02	0.04	0.17	0.30	0.12	0.27

Table 35. Phenotypic correlation coefficients (r_p) among nine traits for the inter-population (BS10 x BS11) in Design II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.22							
Tiller number	0.10	-0.04						
Tiller height	0.03	-0.04	0.51					
Ear length	0.00	-0.05	-0.05	-0.08				
Ear diameter	-0.05	0.03	0.07	0.03	0.08			
Cob diameter	-0.07	-0.12	0.00	0.00	0.16	0.53		
Kernel depth	-0.02	0.12	0.06	0.03	-0.04	0.74	-0.13	
Yield	-0.03	0.29	0.02	0.09	0.30	0.32	0.16	0.24

Table 36. Error correlation coefficients (r_e) among nine traits for the inter-population (BS10 x BS11) in Design II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.03							
Tiller number	-0.06	0.04						
Tiller height	0.03	0.00	0.25					
Ear length	-0.04	-0.03	0.08	0.05				
Ear diameter	-0.05	0.00	0.08	0.04	0.47			
Cob diameter	-0.01	-0.02	0.02	0.00	0.34	0.46		
Kernel depth	-0.06	0.02	0.05	0.03	0.23	0.70	-0.25	
Yield	-0.17	0.12	0.07	0.11	0.44	0.35	0.20	0.23

Table 37. Additive genetic correlation coefficients (r_A) among nine traits for the interpopulation (BS10 x BS11) in combined DI and DII

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.35							
Tiller number	-0.05	-0.18						
Tiller height	0.02	-0.09	0.95					
Ear length	0.09	-0.05	0.08	-0.03				
Ear diameter	0.12	0.22	0.00	-0.04	-0.25			
Cob diameter	0.04	0.13	-0.02	-0.08	0.10	0.68		
Kernel depth	0.08	0.29	0.04	0.06	-0.44	0.77	0.06	
Yield	0.28	0.70	-0.10	0.03	0.23	0.39	0.14	0.41

Table 38. Genotypic correlation coefficients (r_G) among nine traits for the inter-population (BS10 x BS11) in combined DI and DII

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.30							
Tiller number	0.20	-0.04						
Tiller height	0.04	-0.07	0.83					
Ear length	0.02	-0.05	-0.14	-0.25				
Ear diameter	-0.07	0.01	0.04	0.00	-0.19			
Cob diameter	-0.15	-0.27	-0.02	0.01	0.01	0.60		
Kernel depth	0.01	0.18	0.07	0.00	-0.26	0.79	-0.01	
Yield	0.11	0.48	-0.01	0.05	0.17	0.28	0.10	**0.26**

Table 39. Phenotypic correlation coefficients (r_p) among nine traits for the inter-population (BS10 x BS11) in combined DI and II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.19							
Tiller number	0.52	0.04						
Tiller height	0.19	-0.01	0.79					
Ear length	-0.14	-0.15	-0.23	-0.45				
Ear diameter	-0.52	-0.86	0.12	0.22	-0.17			
Cob diameter	-0.98	-1.67	0.08	0.34	-0.21	0.24		
Kernel depth	-0.05	-0.09	0.05	0.05	-0.08	0.87	-0.26	
Yield	-0.16	0.13	0.03	0.03	0.13	0.17	-0.20	0.25

Table 40. Error correlation coefficients (r_e) among nine traits for the inter-population (BS10 x BS11) in combined DI and II

Traits	Traits							
	Days to silk	Ear height	Tiller number	Tiller height	Ear length	Ear diameter	Cob diameter	Kernel depth
Ear height	0.28							
Tiller number	-2.19	-0.42						
Tiller height	-0.05	-0.02	-0.14					
Ear length	0.19	0.06	1.51	0.35				
Ear diameter	0.49	0.79	-1.16	-0.21	0.30			
Cob diameter	0.51	0.65	-0.63	-0.24	0.47	0.83		
Kernel depth	0.13	0.39	-0.43	-0.01	-0.10	0.58	0.05	
Yield	0.18	0.47	0.31	0.14	0.58	0.52	0.35	0.41

number in all designs (r_A = 0.93 to 0.95). High correlations were also obtained between kernel depth and ear diameter (r_A = 0.77 to 0.80), cob diameter and ear diameter (r_A = 0.59 to 0.68), and days to silk and ear height (r_A = 0.32 to 0.36). There were substantial negative correlations between kernel depth and ear length (r_A = -0.32 to -0.53), and ear diameter and ear length (r_A = -0.22 to -0.33) for all designs. Relatively similar trends were shown for the total genetic correlations (r_G), with the highest correlations obtained between tiller height and tiller number (r_G = 0.79 to 0.83) followed by these pairs of traits: kernel depth and ear diameter (r_G = 0.67 to 0.79), cob diameter and ear diameter (r_G = 0.60 to 0.78), and days to silk and ear height (r_G = 0.30 to 0.32).

Both phenotypic (r_P) and error (r_e) correlations show similar trends; kernel depth and ear diameter show the highest correlations with each other in all designs (r_P = 0.69 to 0.87; r_e = 0.58 to 0.71), followed by cob diameter and ear diameter (r_P = 0.24 to 0.71; r_e = 0.46 to 0.83). However, except for tiller number in a few instances, similar correlation coefficients were obtained for r_A, r_G and r_P.

Ear height was the highest correlated trait with yield (r_A = 0.79, 0.63 and 0.70, for DI, DII and DI,II, respectively, Table 41). Among the yield components measured (Table 42), ear diameter (r_A = 0.33 to 0.47) and kernel depth (r_A = 0.35 to 0.44) were the highest correlated traits with yield,

Table 41. Additive genetic (r_A), dominance (r_D), genotypic (r_G), phenotypic (r_P), and error (r_e) correlation coefficients between yield and four traits for the interpopulation (BS10 x BS11) in Design I, Design II, and Design I,II combined

Traits	Design	Correlation coefficients				
		r_A	r_D	r_G	r_P	r_e
Days to silk	DI	0.33	0.25	0.27	0.12	0.04
	DII	0.16	-0.05	0.12	-0.03	-0.17
	DI,II	0.28	-1.82	0.11	-0.16	0.18
Ear height	DI	0.79	0.61	0.66	0.37	0.18
	DII	0.53	0.41	0.50	0.29	0.12
	DI,II	0.70	-0.69	0.48	0.13	0.47
Tiller number	DI	-0.21	0.10	0.02	0.06	0.09
	DII	-0.06	0.17	-0.02	0.02	0.07
	DI,II	-0.10	0.19	-0.01	0.03	0.31
Tiller height	DI	-0.04	0.20	0.14	0.13	0.13
	DII	0.04	0.02	0.04	0.09	0.11
	DI,II	0.03	0.10	0.05	0.03	0.14

followed by ear length with smaller coefficients (r_A = 0.16 - 0.23). All the yield components had greater error correlations than the other traits measured. This result shows that there are greater effects of the environment on the associations between the yield components and yield itself. All other traits studied had very small correlation coefficients among each other and with yield.

Table 42. Additive genetic (r_A), dominance (r_D), genotypic (r_G), phenotypic (r_P), and error (r_e) correlation coefficients between yield and four traits for the interpopulation (BS10 x BS11) in Design I, Design II, and Design I,II combined

Traits	Design	Correlation coefficients				
		r_A	r_D	r_G	r_P	r_e
Ear length	DI	0.22	0.37	0.33	0.45	0.53
	DII	0.16	0.21	0.17	0.30	0.44
	DI,II	0.23	-0.13	0.17	0.13	0.58
Ear diameter	DI	0.47	0.24	0.30	0.43	0.50
	DII	0.33	0.20	0.30	0.32	0.35
	DI,II	0.39	-0.98	0.28	0.17	0.52
Cob diameter	DI	0.23	0.11	0.14	0.26	0.34
	DII	0.04	0.49	0.12	0.16	0.20
	DI,II	0.14	-0.14	0.10	-0.20	0.35
Kernel depth	DI	0.44	0.27	0.32	0.35	0.35
	DII	0.35	-0.21	0.27	0.24	0.23
	DI,II	0.41	-0.57	0.26	0.25	0.41

D. Progress from Reciprocal Full-sib Selection

The estimates of interpopulation genetic variance components obtained and reported in section V B were used to compute the expected progress from reciprocal full-sib selection (RFS) using the formula described in section IV G. Three values were obtained for the expected gain (G) per cycle because three estimates obtained from the three designs used (DI, DII and DI,II) were utilized in calculating G. Because the proportions of testcrossed progenies selected differed from cycle

to cycle, the different resulting selection intensities (K) in Table 50 of the Appendix were used in the calculations for respective cycles. The values for K were obtained by extrapolation from the graph of Falconer (1960). To determine the relative progress made in the population improvement phase of the RFS scheme, entries of the original populations and their crosses and the most advanced cycle of the populations and their cross were yield tested in replicated trials to monitor their response to selection for yield and other agronomic traits. Table 43 shows the mean yields of the population and interpopulation cycles showing progress from RFS.

The population crosses of $C_1 \times C_1$, $C_2 \times C_2$ and $C_3 \times C_3$ show improvements over the original population cross $C_0 \times C_0$ (6.5%, 5.3%, and 22.2%, respectively). The mean difference between the $C_0 \times C_0$ and $C_3 \times C_3$ ($\bar{d} = 13.7$) was significant (5% probability level). This trend coincides with the expected increases in yield for all designs, although the observed increase of $C_3 \times C_3$ over the $C_0 \times C_0$ (22.2%) was lower than the expected (37.4% for DI; 36.9% for DII, and 38.0% for DI,II). However, the observed increase from $C_2 \times C_2$ to $C_3 \times C_3$ (16.0%) was higher than the expected (12% for all designs). This increase from $C_2 \times C_2$ to $C_3 \times C_3$ was the highest observed increase, after the decrease in yield (-1.1%) from $C_1 \times C_1$ to $C_2 \times C_2$. Similar significant improvements were made in the populations themselves. Increases in yield of 17.1% and 16.6% were observed for the BS10(FR)C_3 over the C_0 and BS11(FR)C_3

Table 43. Mean yields of population and interpopulation cycles showing progress fro from reciprocal full-sib selection in an interpopulation of maize (BS10 x BS11)

Inter-population	Observed increase			Expected increase								
				DI			DII			DI,II		
	q/ha	%[a]	%[b]	q/ha	%[a]	%[b]	q/ha	%[a]	%[b]	q/ha	%[a]	%[b]
$C_0 \times C_0$	61.8	-	-	-	-	-	-	-	-	-	-	-
$C_1 \times C_1$	65.8	6.5	6.5	68.2	10.3	10.3	68.1	10.2	10.2	68.3	10.5	10.5
$C_2 \times C_2$	65.1	5.3	-1.1	75.8	22.7	11.1	75.6	22.3	11.0	76.0	23.0	11.3
$C_3 \times C_3$	75.5	22.2	16.0	84.9	37.4	12.0	84.6	36.9	11.9	85.3	38.0	12.2
Population												
BS10(FR)C_0	55.7	-										
BS10(FR)C_3	65.2	17.1										
BS11(FR)C_0	58.5	-										
BS11(FR)C_3	68.2	16.6										

[a] % increase over $C_0 \times C_0$.

[b] % increase over the immediate previous cycle.

over the C_0, respectively ($\bar{d} = 9.5 \pm 3.0$ for BS10, and 9.7 ± 3.0 for BS11; Hallauer, 1976). The increases in the population cycles *per se* were, however, lower than the increases observed in the interpopulation cycles.

VI. DISCUSSION

The results I have reported were based on several assumptions related to the several sections of my study. Assumptions were made in respect to the experimental design used, the matings themselves, and the translation of information from the design variance components to genetic information in terms of the genetic variance components. It is the genetic information that is useful in determining the type of gene action and amount of genetic variability present within the population, which is subjected to recurrent selection. The reference population in my study is the interpopulation formed by crossing two composite maize populations, BS10 x BS11. The genetic variance components estimated in my study would characterize the reference interpopulation, which was generated from a reciprocal full-sib selection program. In a reciprocal full-sib selection scheme as proposed by Hallauer (1967a, b) and Lonnquist and Williams (1967), selections are based on the performance of testcross (full-sib) progenies. Such full-sib testcrosses were made by mating particular males from one population to particular females of a second population, with each population serving as a tester for the other.

A. Validity of Assumptions

Sampling variance is the expected problem in a Design I scheme when S_0 plants, with inbreeding coefficient (F) of

zero are used in the matings. It is assumed that such a problem would be removed by crossing one male plant from the male row to several plants within each of the rows designated as females. Adequate sample size, of the magnitude described by Marquez-Sanchez and Hallauer (1970a), was used. One single male plant was crossed to each of six female plants. On the whole, 80 males were each crossed to six females, resulting in 480 Design I (DI) progenies. It also is assumed that the inbred lines used in Design II matings were random samples from the original populations and had inbreeding coefficients (F) of one. In my study, the random inbred lines used were in the S_7 generation with the expected value of F = 0.992, which is approximately one, thus having little or no deviation from the expectations. There also was no intentional selection in the development of the inbred lines. Therefore, with the methods used in the matings, and a comparison of the means for all traits between DI and DII progenies (Table 19) which showed good agreement, the assumption of unintentional selection and randomness was supported and the assumption of good sampling seems valid.

In the experimental design and field layout there was the assumption that competition, plot-to-plot environmental variation and within plot variation were the same for the genetically heterogenous DI progenies and the homogenous DII plant progenies. This assumption was of no problem in my study because of the field layout used (described in section III B) and

general vigor and performance of the Design I and II full-sib progenies were similar for both mating designs (Table 19).

In the combined analysis of my data for the estimation of variance components, I described the first-order interactions, genotype x year and genotype x location, with the second-order interaction genotype x year x location, as genotype x environment interaction. The environments (location x year) were also treated as random. Although the first-order interactions were significant, they were still smaller than the second-order interaction, as indicated by Robinson and Moll (1959) and Comstock and Moll (1963). The confounding effects of the locations and years will therefore be small in the estimate of genotype x location x year effect. In terms of estimating genetic variances and genotype x environment interaction variances when each year and location effects and their interactions were treated as random, Hanson (1964) indicated that the bias that would be introduced was of little importance. Therefore, the confounding should not be of much concern in this study with respect to the estimates.

Several assumptions were made in the translations of covariances among full-sib and half-sib relatives in terms of genetic variances. It was assumed that: there is diploid inheritance, no maternal effects or reciprocal differences, no environmental correlations among relatives, and no linkages or there is presence of linkage equilibrium. The nature of inheritance in maize is diploid. This fact is unquestionable

from results of several studies on its genetic mechanism. Generally, maternal effects have not been found to be significant in maize, an indication that the assumption of no maternal effects is valid. Although the literature is inconclusive on the importance of reciprocal differences in maize for several traits, it seems maternal effects are minor in maize. However, in my study, the presence of reciprocal or maternal effects were shown for two traits, tiller number and tiller height (Table 23). Any environmental correlations among relatives in the two designs were removed by the randomization procedure used in the experimental design and field layout.

The assumption of no linkage seems to be invalid to some extent, although it could reasonably be assumed that the two populations used in the study were in linkage equilibrium. Both varieties were maintained by random mating in about 0.4 ha. plots for at least three generations. The S_7 inbred lines used in the DII scheme were developed from the two randomly mating populations. Selfing for several generations to homozygosity has the effect of breaking initial linkages that exist in the original populations. Thus, linkage has no effect when parents are homozygous; therefore, it was not expected that linkage would have any effect on the DII progenies. On the other hand, since S_0 plants ($F = 0$) were used in generating DI progenies, it was expected that some linkage problems would be encountered in DI. Considering the combination of the two mating designs, DI,II, it was expected that there

would not be any consequential linkage bias because the little linkage effect in the estimates from DI progenies would be counteracted by the effects of the estimates from DII progenies, which are free from linkage bias. Theoretically, the effect of linkage is to bias upwards estimates of σ^2_A (when in coupling phase) and downwards (when in repulsion phase). Estimates of σ^2_D are overestimated regardless of the linkage phase. In my study, except for few negative estimates of σ^2_D, most of the traits (excepting tiller number and tiller height) had DI estimates of σ^2_A and σ^2_D higher than the estimates in DII. Since linkage bias exists in DI, I could infer that σ^2_A and σ^2_D in DI were overestimated because of linkage bias.

B. Comparison of Estimates of Genetic Variances

Three different estimates of variance components were computed in this study. For all the traits (except cob diameter) and considering the three different estimates, σ^2_A was of the greatest magnitude. In most instances (except for tiller number, cob diameter, and yield), it accounted for 75% or more of the total genetic variability. There were, however, some differences between the three estimates of the various components (Table 25 and Table 26). In the estimates of σ^2_A, except for ear diameter, cob diameter and yield, the combined DI,II estimates lie within the limits of the individual design (DI and DII) estimates. This observation would indicate that a combination of the two mating designs, DI and

DII, for the calculation of genetic variance estimates, would be a better procedure than from the designs individually. Its being better did not make it free from problems. The principal problem evolving from the use of the combined DI,II was the higher standard errors (higher than any of the individual designs) associated with all the combined estimates of the components of variance.

My results show that in the interpopulation, additive genetic variance component was at least twice (or more than twice in most instances) than the dominance variance (σ^2_D/σ^2_A = 53% for DI, 38% for DII and 37% for DI,II for yield). This observation conflicts with that of Stuber (1965) working with an interpopulation of two different varieties, Jarvis and Indian Chief, in North Carolina. His results indicated that the magnitudes of the additive variance and the dominance variance differ very little for yield. On the other hand, Robinson and Comstock (1955) obtained similar results for yield, as in my study, with the same trend in the magnitudes of σ^2_A and σ^2_D and the ratio, σ^2_D/σ^2_A, for three maize hybrid populations using the DI.

The high value of 90% obtained for the ratio, σ^2_D/σ^2_A, for cob diameter, indicating almost equal magnitudes of $\sigma^2_{A(12)}$ and $\sigma^2_{D(12)}$ for the trait, could be due to overestimation of $\sigma^2_{A(12)}$ because of linkage bias in DI. The DII estimate for the same trait was observed to be comparatively smaller (13%). Few estimates of interpopulation σ^2_D were negative. Two

negative estimates of σ^2_D were obtained in DI for ear height and kernel depth, and four were obtained for days to silk, ear height, ear diameter and cob diameter in DI,II combined. The occurrence of negative estimates of genetic variances have been frequently reported in the literature, especially for Design I. These negative estimates could be due to several factors including: sampling variance, assortative mating, linkage, deficiency in the genetic model, and estimates of actual zero values. The fact that they could be true zero or very small values is deduced from the relatively large standard errors associated with some of the estimates. Large standard errors coupled with negative estimates also could be a result of sampling variation due to insufficient sampling in the basic populations, as postulated by Marquez-Sanchez and Hallauer (1970a and 1970b). In their intrapopulation study, using the DI scheme, Marquez-Sanchez and Hallauer (1970a and 1970b) concluded that mating at least four females to one male or ideally mating six to eight females to one male was adequate sampling; at least 48 males should be used in the matings. In my study, six females were mated to one male and total of 80 males were used in the DI mating scheme. Therefore, I expected no sampling variance problem; actually, good sampling was obtained as indicated by the very similar results obtained between DI and DII progenies in Table 19. Consequently, inadequate sampling seems not a problem in my study and the occurrence of negative estimates of $\sigma^2_{D(12)}$ and $\sigma^2_{DE(12)}$.

Another possible reason for negative estimates of dominance variance could be assortative mating, as indicated by Lindsey, Lonnquist and Gardner (1962). This procedure of mating early flowering males to early flowering females could result in the overestimation of $\sigma^2_{f/m}$ and a negative estimate of σ^2_D for silking date and its correlated traits. In my study, we tried to minimize assortative mating by delayed planting of the males. Thus, assortative mating should not be a serious problem in this study, although negative estimates of $\sigma^2_{D(12)}$ and $\sigma^2_{DE(12)}$ appeared for ear height (a trait correlated with silking date in my studies) and days to silk, respectively. As earlier indicated, the effect of linkage bias would be on DI estimates. When in coupling phase, linkage tends to bias estimate of σ^2_A upwards; this could give negative estimates of σ^2_D, as illustrated from the relationship of $4(\sigma^2_{f/m} - \sigma^2_m) = \sigma^2_D$, where $\sigma^2_A = 4\sigma^2_m > 4\sigma^2_{f/m}$. In my study, therefore, a major reason for occurrence of negative $\sigma^2_{D(12)}$ and $\sigma^2_{DE(12)}$ estimates could be linkage bias.

Apart from ear height, tiller number and tiller height, all DI estimates of $\sigma^2_{DE(12)}$ for days to silk, yield and the yield components were negative. There was no definite trend in comparing the additive x environment interaction variance, $\sigma^2_{AE(12)}$, with the dominance x environment interaction variance, $\sigma^2_{DE(12)}$. Some estimates of $\sigma^2_{AE(12)}$ were larger than those of $\sigma^2_{DE(12)}$ (ear height, tiller number, ear length and yield), while some estimates of $\sigma^2_{DE(12)}$ also were larger than those of

$\sigma^2_{AE_{(12)}}$ (days to silk, tiller height, ear diameter and kernel depth). In general, if the estimates were divided by their respective standard errors (Appendix Table 48), it was observed that ear height, tiller number, and yield showed the greatest interactions ($\sigma^2_{AE_{(12)}}$) with the environments, while tiller height and kernel depth showed the least interaction with environment.

For all traits studied, except yield, the pooled error variances for DI ($\sigma^2_{(12)}1$) were greater than error variances for DII ($\sigma^2_{(12)}2$). This observation agrees with the expected because the plots in DI are heterogenous, while those in DII are homogenous. The genetic sampling of plants in the DI plots may have contributed to the larger experimental errors of the DI scheme.

All estimates of variances calculated in DI', DI, DII, and DI,II combined, for all traits, can be compared in general terms of the designs. The DI estimates agreed more closely than DI' estimates with the DII estimates. It seemed that the values obtained for DI' by the theoretical considerations $\frac{1}{2}(\sigma^2_{A_{12}} + \sigma^2_{A_{21}}) = \frac{1}{2}\sigma^2_{A_{(12)}}$, were overestimations of the genetic variation present in the interpopulation. Comparing the DI, DII, and DI,II combined estimates, the combination of the two designs, DI,II, agreed more with the DI than the DII estimates. This may have occurred because there were more progenies tested in DI (480) compared to DII (320), so that when the estimates were pooled over the two designs in DI,II,

the pooled degrees of freedom would be proportionately greater in the DI. Therefore, the biases of estimates in DI,II combined would tend towards the biases of DI estimates. Most of the estimates for traits studied in DI,II were associated with relatively high standard errors. This might be a result of the matrix procedure used in combining the mean squares followed by the least squares method in solving the resulting equations to obtain the parameter estimates.

Finally, when the several estimates obtained were weighted by dividing them with their respective standard errors (Appendix Table 48), four main features were observed within the interpopulation: days to silk (maturity), ear height, and ear diameter had the greatest additive genetic variance; genetic variation was lowest for yield; ear height, tiller number, and cob diameter had greater dominance variance, while kernel depth had the least dominance effects; and the error variance was substantially reduced by combining DI and DII.

C. Interpopulation Correlations

Within the interpopulation, the correlations among the traits having the greatest associations were obtained between tiller height and tiller number, ear height and yield, and ear height and ear diameter. Ear diameter also was highly associated with cob diameter and with kernel depth. However, an appreciable negative association was observed between ear length and kernel depth. Among the yield components, ear

diameter and kernel depth were the most important. There was a slight indication of a negative association between number of tillers and yield.

D. Expected Versus Observed Progress from Reciprocal Full-sib Selection

Predicted changes for grain yield in the interpopulation differ from cycle to cycle because different proportions were selected within successive cycles. The expected percentage increase of later cycles was more than immediate previous cycles because stricter selection pressures were exerted on the later cycles (Appendix Table 50). Generally, the observed gains in yield followed the same pattern as for the expected in the improved population crosses, and also in the populations _per se_.

The observed increases in yield of improved population crosses after three selection cycles (22%) over the original population cross ($C_0 \times C_0$) agreed to some extent with the predicted (37 to 38% in Table 43). The discrepancies could be a reflection of the relatively high additive x environmental interaction variance as compared to the additive genetic variation. The effect of this increase of $\sigma^2_{AE_{(12)}}$ was to inflate the values of the predictions (Table 43). In the presence of a large $\sigma^2_{AE_{(12)}}$, response to selection could be made to be more consistent with expectations by making selections based on evaluation in more environments. It may well

be that the lack of complete agreement between the observed and expected increases in yield was due to the fact that the procedure used to compute the expected response did not take into account changes in genetic variance among testcrosses associated with selection. However, it is known that there is no appreciable change in gene frequencies in early generations with selection for complex traits such as yield. It is expected that the estimates for the original interpopulation would be valid for the first three cycles of selection because the changes in gene frequency are expected to be small.

In Table 43, a small decrease in gain (-1.0%) was observed from the first cycle to the second cycle of interpopulation selection. This might have been the reason for the greater observed increase in yield (16.0%) than predicted (12.0%) from cycle two ($C_2 \times C_2$) to cycle three ($C_3 \times C_3$). Sampling error of the plants included in the interpopulations evaluated also could contribute to the differences noted between the expected and observed means.

VII. SUMMARY

My investigation was based on three main objectives, namely: (1) to estimate the amount and type of genetic variability in an interpopulation of maize (BS10 x BS11); (2) to utilize the estimates obtained for computing the expected genetic change in the two populations due to interpopulation selection; and (3) to compare the predicted response with the observed gain.

I used two mating designs, the nested (Design I) and crossed classification (Design II) mating designs, and a combination of the two designs (Design I,II). The reference population used for defining the genetic parameters was the interpopulation formed by crossing random individuals in pairs from two parent populations. A genetic model of only additive and dominance effects was used. Genetic variability in the interpopulation was partitioned into additive and dominance components with their interactions with the environment. Since the gene frequencies of the parent populations were not known, the procedures used in estimating genetic parameters in the interpopulation were patterned along that used for intrapopulations. Covariances among half-sibs and full-sibs were, however, interpreted in terms of interpopulation genetic variances.

Data were collected on nine traits, including: number of days to silk, ear height, tiller number, tiller height, ear

length, ear diameter, cob diameter, kernel depth, and yield. For the interpopulation, the results showed that additive genetic variance ($\sigma^2_{A_{(12)}}$) was the most important component of genetic variability for all traits. Dominance variance ($\sigma^2_{D_{(12)}}$) was about half the additive variance for tiller number and yield. Except for yield, estimates of additive x environment interaction variance ($\sigma^2_{AE_{(12)}}$) was much lower than their corresponding $\sigma^2_{A_{(12)}}$ for all traits. There was no definite trend in estimates of dominance x environment interaction variance ($\sigma^2_{DE_{(12)}}$) when compared with corresponding $\sigma^2_{D_{(12)}}$. Estimates of variance components in the combined DI,II tend to be biased towards the DI estimates.

The three estimates of the correlation coefficients among traits, using variance and covariance components estimated from the designs, DI, DII and DI,II, showed that ear height was the most highly correlated trait with yield. Among the four yield components measured, ear diameter and kernel depth were equally important. Predictions using interpopulation variance components showed agreement, trendwise, between the expected and observed gain in yield. After three cycles of reciprocal full-sib selection, there was an observed gain of 22% in the $C_3 \times C_3$ interpopulation compared to the original $C_0 \times C_0$ population; the predicted genetic gain was 37%. An observed gain of 17% in the two parent populations also was realized. This confirmed the effectiveness of the reciprocal full-sib selection method in improving maize populations and their crosses.

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X. APPENDIX

Components of variance		
$\sigma^2_{f/m^1_{21}}$	$\sigma^2_{1_{12}}$	$\sigma^2_{1_{21}}$
1.02 ± 0.15	2.47 ± 0.13	3.10 ± 0.17
58.43 ± 6.73	68.97 ± 3.21	51.46 ± 2.40
3.62 ± 0.45	7.87 ± 0.37	4.96 ± 0.23
636.99 ± 115.11	3647.79 ± 169.89	3323.51 ± 154.79
51.48 ± 7.41	189.00 ± 8.80	164.27 ± 7.65
1.58 ± 0.20	7.05 ± 0.33	3.72 ± 0.17
0.78 ± 0.10	2.95 ± 0.14	1.98 ± 0.09
0.62 ± 0.10	3.41 ± 0.16	2.70 ± 0.13
69.45 ± 14.06	478.50 ± 23.22	432.48 ± 20.14

Table 45. Estimates of genotype x environment interaction variances[a] and their standard errors for the two groups of interpopulation progenies (12 and 21 in Design I

Trait	Components of variance			
	$\sigma^2_{ml^1_{12}}$	$\sigma^2_{ml^1_{21}}$	$\sigma^2_{f/ml^1_{12}}$	$\sigma^2_{f/ml^1_{21}}$
Days to silk	0.05 ± 0.04	0.09 ± 0.07	-0.41 ± 0.09	0.13 ± 0.15
Ear height	5.48 ± 1.72	2.41 ± 1.29	1.10 ± 2.61	10.37 ± 2.40
Tiller number	0.92 ± 0.26	0.43 ± 0.15	1.02 ± 0.34	0.83 ± 0.22
Tiller height	102.11 ± 64.81	8.99 ± 52.44	92.06 ± 139.33	279.03 ± 136.03
Ear length	5.95 ± 2.84	0.06 ± 2.32	-18.36 ± 6.22	5.41 ± 6.33
Ear diameter	0.16 ± 0.08	0.10 ± 0.06	-1.51 ± 0.20	-0.30 ± 0.12
Cob diameter	0.06 ± 0.03	0.05 ± 0.03	-0.59 ± 0.09	-0.18 ± 0.07
Kernel depth	0.07 ± 0.05	0.04 ± 0.04	-0.12 ± 0.12	-0.05 ± 0.10
Yield	53.32 ± 14.58	43.63 ± 13.22	15.18 ± 19.16	49.87 ± 18.35

[a]The symbols $\sigma^2_{ml^1_{12}}$ and $\sigma^2_{ml^1_{21}}$ denote the male x environment interaction variances for population 1 x population 2 (12), and population 2 x population 1 (21), respectively, in DI; and $\sigma^2_{f/ml^1_{12}}$ and $\sigma^2_{f/ml^1_{21}}$ denote the female within male x environment interation variances for (12) and (21), respectively, in DI.

Components of variance			
$\sigma^2_{f_{(12)}}$	$\sigma^2_{mf_{(12)}}$	$\sigma^2_{1\ (12)}$	$\sigma^2_{2\ (12)}$
1.00±0.21	0.32±0.06	2.79±0.11	1.24±0.06
71.74±14.42	17.09±2.52	60.22±1.98	45.47±1.77
7.21±1.46	1.60±0.27	6.41±0.21	5.81±0.23
807.92±187.86	348.21±87.41	3485.65±114.86	3549.86±4.36
78.51±17.05	27.25±4.70	176.64±5.82	112.12±4.36
2.10±0.42	0.30±0.09	5.39±0.18	3.22±0.13
0.76±0.16	0.18±0.04	2.46±0.08	1.74±0.07
1.24±0.25	0.09±0.06	3.06±0.10	2.80±0.11
115.48±31.36	67.02±15.82	465.49±15.36	525.66±20.45

Table 47. Estimates of genotype x environment interaction variances[a] and their standard errors for the interpopulation (BS10 x BS11) in DI and DII

Trait	Components of variance				
	$\sigma^2_{ml^1_{(12)}}$	$\sigma^2_{ml^2_{(12)}}$	$\sigma^2_{f/ml^1_{(12)}}$	$\sigma^2_{fl^2_{(12)}}$	$\sigma^2_{fml_{(12)}}$
Days to silk	0.07±0.04	0.15±0.05	-0.14±0.08	0.05±0.04	0.22±0.07
Ear height	3.95±1.07	5.62±1.35	5.73±1.77	9.98±1.79	3.78±1.84
Tiller number	0.67±0.15	1.53±0.26	0.92±0.20	1.22±0.23	0.76±0.25
Tiller height	55.35±41.63	190.59±71.88	185.55±97.39	117.86±64.88	4.21±128.24
Ear length	3.00±1.83	8.07±2.78	-6.48±4.43	20.30±3.99	10.20±4.58
Ear diameter	0.13±0.05	0.23±0.09	-0.90±0.11	0.17±0.08	0.51±0.14
Cob diameter	0.05±0.02	0.12±0.04	-0.39±0.05	0.17±0.04	-0.03±0.06
Kernel depth	0.06±0.07	0.17±0.07	-0.08±0.08	0.12±0.07	0.42±0.12
Yield	48.47±9.88	72.23±16.34	32.53±13.26	80.62±17.18	45.51±21.34

[a]The symbols $\sigma^2_{ml^1_{(12)}}$ and $\sigma^2_{ml^2_{(12)}}$ denote the interpopulation male x environment interaction variance in DI and DII, respectively; $\sigma^2_{f/ml^2_{(12)}}$ and $\sigma^2_{fl^2_{(12)}}$ denote the interpopulation female x environment interaction variance in DI and DII, respectively; $\sigma^2_{fml_{(12)}}$ denotes the male x female x environment interaction variance in DII.

Table 49. Estimates of error variance ($\sigma^2_{(12)}$) in the interpopulation for nine traits in the two designs, DI and DII, and their combination, DI,II

Traits	Estimates		
	DI	DII	DI,II
Days to silk	2.79 ± 0.11	1.24 ± 0.06	3.56 ± 0.22
Ear height	60.22 ± 1.98	45.47 ± 1.77	219.46 ± 13.20
Tiller number	6.41 ± 0.21	5.81 ± 0.23	4.33 ± 0.51
Tiller height	3485.65 ± 114.86	3549.86 ± 138.07	3657.52 ± 298.45
Ear length (x 10^2)	176.64 ± 5.82	112.12 ± 4.36	171.71 ± 10.07
Ear diameter (x 10^2)	5.39 ± 0.18	3.22 ± 0.13	5.09 ± 0.41
Cob diameter (x 10^2)	2.46 ± 0.08	1.74 ± 0.07	3.24 ± 0.21
Kernel depth (x 10^2)	3.06 ± 0.10	2.80 ± 0.11	2.23 ± 0.16
Yield	465.49 ± 15.34	525.66 ± 21.44	482.70 ± 39.91

Table 50. Selection intensity (K) used in the different interpopulation cycles for RFS in BS10 x BS11

Interpopulations	Proportion selected (%)	K
$C_0 \times C_0$	13.9	1.60
$C_1 \times C_1$	11.0	1.73
$C_2 \times C_2$	8.0	1.86