

COMPARISON OF S<sub>2</sub> PROGENY AND INBRED TESTER METHODS  
FOR<sup>2</sup> IMPROVEMENT OF MAIZE

By  
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A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF  
THE UNIVERSITY OF FLORIDA IN PARTIAL  
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA  
1977

To  
the memory of my mother, Weizero Zenebu Tirfe,  
and father, Grazmach Ameha Meshesha.

## ACKNOWLEDGMENTS

The author expresses his deepest thanks to Dr. Earl S. Horner, the chairman of his supervisory committee, for his constructive guidance in the research and preparation of the manuscript. The author also expresses appreciation to the members of his supervisory committee, Dr. Charles E. Dean, Dr. Wayne B. Sherman, Dr. Victor E. Green, and Dr. Vincent N. Schroder for serving on the supervisory committee and for their helpful suggestions for improving the content and structure of the dissertation.

Thanks are extended to Dr. Frank G. Martin for his help in the analyses of the data, Mr. Vernon R. Munden for his assistance in the field work, and some colleagues who helped him in recording data. The author is indebted to his fiancée Miss Birhan Tekabe for her encouragement and assistance in typing.

The author thanks Dr. Dagnatchew Yirgou, who was the General Manager of the Institute of Agricultural Research, Ethiopia, for allowing him to continue his studies. Thanks are also due to the Food and Agriculture Organization of the United Nations for the financial assistance during the study program.

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Abstract of Dissertation Presented to the  
Graduate Council of the University of Florida in Partial Fulfillment  
of the Requirements for the Degree of Doctor of Philosophy

COMPARISON OF  $S_2$  PROGENY AND INBRED TESTER METHODS  
FOR IMPROVEMENT OF MAIZE

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March, 1977

Chairman: Dr. Earl S. Horner  
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The Inbred Tester and  $S_2$  Progeny Methods have been used effectively for improving maize (Zea mays L.) populations. However, it is very important for a breeder to know which one of these methods is more effective. Theoretically, the  $S_2$  Progeny Method is more effective than the Inbred Tester Method since the genotypic variances that are due to additive effects are expected to be much larger among  $S_2$  progenies than among half-sib progenies, but up to now, the two methods have not been compared together in the field. In 1975, however,  $S_2$  lines of two populations, A and B, were evaluated for yield by the Inbred Tester Method and by the  $S_2$  Progeny Method and seeds were made available for study.

High and low yield groups of 10 lines each were selected by each method from the A and B populations and seeds were grown to make the evaluation by (1) out crossing to the original inbred testers and to two unrelated hybrid testers, (2) yield of synthetics, and (3) interpopulation crosses. Ears were harvested separately and seeds were bulked to make 40 composites (24 for testcrosses, 8 for synthetics, and 8 for interpopulation crosses),

The evaluation tests were planted at two locations near Gainesville with 90 x 30 cm spacings. A split-plot design with 10 replications was used to test the testcrosses, a randomized complete-block design with 15 replications was used to test the synthetics, and another randomized complete-block design with 10 replications was used to test the inter-population crosses at each of the two locations. Data on yield and other characteristics were collected and analyzed.

The testcross results indicate that both methods were equally effective in selecting lines for high combining ability, but the Inbred Tester Method was more effective in selecting lines for low combining ability with the unrelated doublecrosses. The synthetics and the inter-population crosses showed no significant difference between methods. These results show that lines selected by the Inbred Tester Method can combine well with unrelated populations and crosses between lines of Populations A and B should result in higher grain yields.

The inbred testers detected small differences in combining ability among selected  $HS_2$  and  $LS_2$  groups better than the doublecross testers. This indicates that the inbred testers would be effective in improving frequency of favorable genes having additive effects.

Correlated responses of other characteristics to selection for high and low grain yield were somewhat different for the two methods.

## INTRODUCTION

During the period 1896 to 1917 mass selection and ear-to-row methods, both of which involve recurring cycles of selection, were frequently used in corn (Zea mays L.) improvement. In the second decade of the 20th century, however, these methods were found to be ineffective for improving yield. These failures were probably due to visual selection for uniformity of ear types, which resulted in inbreeding, and to poor experimental plot techniques. When work began on hybrid development, population improvement was neglected for many years. But, after plot techniques were improved and adequate additive genetic variation for yield was found in most populations, population improvement was re-emphasized. Gardner (1961), Weibel and Lonnquist (1967), and others reported significant improvement using the mass and ear-to-row methods of selection.

During the 1910 to 1950 period, conventional inbreeding to produce homozygous lines together with systematic determination of the best combinations for hybrids (evaluation for general combining ability, GCA, and specific combining ability, SCA) became important without emphasis on rapidly recurring cycles of selection. However, Hull (1945) emphasized the advantage of recurring cycles, which have multiplicative effects, for high yield and suggested selection for SCA directly using an inbred line as a tester. He assumed that additive genetic variation in adapted varieties used was less important than non-additive variation. Since then, others followed with suggestions for alternative methods, among which reciprocal recurrent selection (RRS), full-sib, half-sib, and selfed

progeny selection were important. Yet, there is no general agreement as to which is the best for yield improvement.

In Gainesville, Florida, Robinson (1976) selected high and low yielding  $S_2$  lines in two different populations based on (a) half-sib progeny performance using an  $S_1$  line of each population as a tester of lines from the other and (b)  $S_2$  progeny performance per se. The results showed that among the top yielding 15 lines, six lines in Population A and one line in Population B and among the low yielding ten lines, two lines in Population A and one line in Population B were selected by both methods. This indicates that the two methods are quite different in indentifying lines for grain yield in corn.

The objective of this study was to evaluate the half-sib progeny with an inbred tester and the  $S_2$  progeny per se methods for identifying lines with high and low combining ability for grain yield. The evaluation was made by forming high and low performing groups by each method in each population using Robinson's (1976) data and (a) crossing each group to its respective  $S_1$  tester and to two unrelated commercial hybrids; (b) developing synthetic sub-populations of each group; and (c) crossing different groups from the two populations.

## LITERATURE REVIEW

### Recurrent Selection

Population improvement in corn is now being carried on by many breeders, who use a system generally called recurrent selection (RS). The improvement results from accumulation of favorable genes during recurring cycles. Simple RS is performed by selecting superior plants and making many intercrosses among selected plants or their progenies and is most useful for characters having high heritability. Recurrent selection for GCA (Jenkins, 1940) and SCA (Hull, 1945) employ testcross performances with broad and narrow base testers, respectively. Reciprocal recurrent selection (Comstock et al., 1949) uses two heterozygous populations, each being the tester for lines from the other, simultaneously.

A breeding method similar to RS for GCA was first suggested by Hayes and Garber (1919). They outlined a procedure for developing a synthetic population with high protein content by selfing, selecting, and subsequent crossing. However, this method was not adopted at that time. Later, after Jenkins (1940) presented the first detailed description of the methodology for GCA, many breeders have stressed the importance of a broad base tester since it has been considered superior to narrow base testers for identification of lines which provide greater average performance upon combination with other lines.

Hull (1945) first proposed RS for SCA, and suggested the use of a homozygous lines as a tester. He believed that overdominance was the major

type of gene action present in adapted varieties since additive gene action was presumably exhausted by previous selection. Comstock et al. (1949) proposed and outlined a method for RRS which was considered to be effective regardless of level of dominance present, but it would have maximum efficiency if overdominance or dominance by dominance interaction was present in the populations used. Current theory further suggested that RRS is appropriate whether additive or nonadditive gene action is predominantly present.

The considerable time and progeny testing needed to extract superior homozygous lines encouraged the need for early testing, which essentially helped RS to develop. Jenkins (1935) studied topcross yield results, using lines which represented eight generations of selfing and discarded lines of each generation, and concluded that inbred lines that showed superiority in the early generations of selfing remained relatively stable. Lonnquist (1950) presented conclusive evidence that continued selection and testing after  $S_1$  would be most profitable for those lines exhibiting highest topcross performance in early generations.

#### Gene Action

Partitioning of genetic components of variance based on type of gene action for various mating designs has provided a scale for measuring the inheritance of agronomically useful characters. Robinson et al (1949), Gardner et al. (1953), and others found yield genes in the overdominance range. However, later studies by these workers showed that these estimates of overdominance were due to linkage disequilibrium. Kravenchko et al. (1971) reported that overdominance as well as epistasis was apparent for grain yield; partial to complete dominance was observed for days to silk,

moisture percentage in the grains at harvest, plant height, and ear height. Heterosis occurred for length of growing season, resistance to smut, and number of grains per row. Thompson et al. (1971) showed that additive and dominance parameters were responsible for an average of 90% of the variability in the inheritance of ear height. Tavares (1972) obtained the highest heterosis from those hybrids connected with low yielding parents, and heterosis for yield was not always accompanied by heterosis for characters positively correlated with yield.

#### Half-sib Method and Effectiveness of Testers

The half-sib progeny test, where selected progenies are mated among themselves, uses one-fourth of the additive genetic variance and requires two generations per cycle of selection. Where the selected selfed male or female parents are mated among themselves, it utilizes one-half the additive variance and requires at least three generations per cycle. Improvement by this method not only depends on the genetic constitution of the population but also on the type of tester used. Rawlings and Thompson (1962) crossed six lines classified as high, intermediate, and low yielding to high and low yielding testers and found that a low yielding tester would discriminate more effectively among combining abilities of lines crossed with it than would a high yielding tester. In their theoretical comparison, they showed that when gene frequency of a tester is homozygous recessive at all loci, the genetic variance among testcross progenies is larger and it has an increasing advantage as dominance increases compared to heterozygous testers. Allison and Curnow (1966), from a mathematical approach of the two allele locus, stated that if

partial to complete dominance is of primary importance, a low yielding population selected from the parental variety would be the best tester. Lonquist (1968) showed that the highest yield resulted from the intercrosses of lines selected on the basis of performance with the parental population. Selection on the basis of an unrelated tester resulted in slightly better yield when selected high by low groups were crossed than when high by high groups were crossed. This result suggests that the parental tester emphasizes additive gene action while the unrelated tester emphasizes dominance gene action.

Selection for GCA, which is primarily a function of additive gene action, has historically used broad base testers while selection for SCA, which is primarily a function of nonadditive gene action, used a narrow base tester. However, recent results show that narrow base testers also improve GCA, perhaps even more effectively than broad base testers. Russell et al. (1973) evaluated populations developed from five cycles of recurrent selection for combining ability for yield with the inbred tester B14 in two populations, variety 'ALPH' and the  $F_2$  of (WF9 x B7), by using B14 and BSBB as testers. They obtained an average yield increase of about 3.1 q/ha per cycle in 'ALPH' and about 1.3 q/ha per cycle in (WF9 x B7) using B14 as a tester and about 3.6 q/ha per cycle in 'ALPH' and about 1.5 q/ha per cycle in (WF9 x B7) using BSBB broad base tester. Horner et al. (1973) completed five cycles of RS using an inbred line and the parental population as testers and  $S_2$  progeny performance per se in parallel programs. The 15 populations produced by these methods were evaluated for average combining ability with the parental populations and an unrelated broad base tester. They obtained a 4.4% yield gain per cycle from the Inbred Tester Method compared with 2.4 and 2.0% for the parental tester and  $S_2$  Progeny Methods, respectively. They indicated that the

inbred tester was evidently homozygous recessive at many important loci which would result in more successful selection for dominant favorable alleles than would use of a broad base, heterozygous tester. Walejko and Russell (1976) evaluated the progress of RS in which the inbred HY was the tester for two open pollinated varieties and indicated that the yield gain observed for the HY testcrosses and the population crosses were expressed equally well in testcrosses with unrelated testers.

The significance of the findings [Russell et al. (1973), Horner et al. (1973), and Walejko and Russell (1976)] is that (a) inbred testers are very effective for improving the GCA of a population and (b) the fear that narrow base testers improve only SCA in selected populations was unfounded.

The earliest report on the effectiveness of RRS was made by Douglas et al. (1961). They compared performances of first, second, and third cycle composites of each variety and crosses among them and concluded that selection was slightly effective in accumulating favorable alleles in the first two cycles of 'Ferguson's Yellow Dent' and only in the first cycle of 'Yellow Surcropper'. Average combining ability of the varieties was improved only in the first cycle of selection. Eberhart et al. (1973) evaluated the progress from five cycle of RRS in varieties BSSS and BSCB1 and obtained a linear improvement of 2.7 q/ha (4.6%) per cycle from  $BSSS(R)_n \times BSCB1(R)_n$  population crosses. However, there was no significant change in the parents themselves.

## Theory

### Selection based on Selfed Progeny Performance

Selfing is the major type of mating that changes the genotypic frequency of a formerly random-breeding population. Selfing rapidly reduces a population to homozygosity regardless of the number of heterozygous loci initially present. Let us suppose that randomly selfed  $S_0$  plants were heterozygous (Aa) for all loci. In the first generation,  $S_1$  progenies will be 50% homozygous (AA and aa) and 50% Aa.  $S_2$  progenies of randomly selfed  $S_1$  plants will be 75% AA and aa and 25% Aa. If AA and aa in the  $S_0$  generation are assumed to be at the same proportion as the Aa, then randomly selfed  $S_0$  plants will produce  $S_1$  progenies with 75% AA and aa and 25% Aa and likewise  $S_1$  plants will produce  $S_2$  progenies with 87.5% AA and aa and 12.5% Aa. The gene frequency of  $S_2$  lines will be the same as in the  $S_0$  plants, but the genotypic frequencies will vary depending on the gene frequency of the initial population.

When the  $S_2$  progeny means are compared,

AA will be better than Aa for  $\underline{d} < 1.0$

AA will be better than aa for all values of  $\underline{d}$

AA will be equal to Aa for  $\underline{d} = 1.0$

Aa will be greater than AA for  $\underline{d} > 1.0$

where  $\underline{d}$  is a measure of dominance,  $\underline{d} \geq 0.0$ .

It means that if dominance is less than complete, selection will favor AA genotypes; if dominance is complete, selection will favor both AA and Aa; and if there is overdominance ( $\underline{d} > 1.0$ ), selection will favor Aa alone. But with selfing the frequency of Aa genotypes is low.

Examination of inbreeding and its effect on genetic variation among the selfed progenies is very helpful for understanding the changes that would occur in the selfing series. Maximum inbreeding is obtained when like gametes, A with A or a with a unite and under such conditions the inbreeding coefficient (F) will be one because the gene controlling a particular character is fixed. A random mating population on the other hand has an F value of zero. If a base population with gene frequency  $p = q = 0.5$  is selfed, F values will be as follows:

selfing generation	F values
$S_0$	0.00
$S_1$	0.50
$S_2$	0.75
$S_{\infty}$	1.00

The equation for F with selfing as given by Falconer (1960) is  $F = \frac{1}{2}(1 + F_p)$  where  $F_p$  is the inbreeding coefficient of the parent.

It is observed that the increase of F value is inversely related to the decrease of the frequency of heterozygotes in a selfed series. This relationship can be further understood by looking at the genetic variation of the selfed population. If the AA, Aa, and aa genotypes are coded to have values of 2, 1, and 0, respectively ( $\underline{d} = 0.0$ , additive gene action), the variance of different generations can be shown statistically by the formula,

$$V = \frac{\sum f_i (x_j)^2 - (\sum f_i x_j)^2/n}{n}$$

where  $f_i$  is the genotypic frequency,  $i = 1, 2, 3$

$x_j$  is the genotypic value,  $j = 1, 2, 3$

and n is the sum of the genotypic frequencies,  $n = 1.0$

Therefore, if we start from a random mating population with  $p = q$ ,

$$V_0 = \frac{.25(2)^2 + .5(1)^2 + .25(0)^2 - (1.0)^2/1.0}{1.0} = 0.5$$

$$V_1 = \frac{.375(2)^2 + .25(1)^2 + .375(0)^2 - (1.0)^2/1.0}{1.0} = 0.75$$

$$V_2 = \frac{.4375(2)^2 + .125(1)^2 + .4375(0)^2 - (1.0)^2/1.0}{1.0} = 0.875$$

$$V_\infty = \frac{p^2(2)^2 + 2pq(1)^2 + q^2(0)^2 - (1.0)^2/1.0}{1.0} = 1.00$$

The relationship of  $V$ 's, gene frequency, and inbreeding coefficients in the selfed series is,

<u>V in selfed generations</u>	<u>V values</u>	<u>V in terms of gene frequencies</u>	<u>V in terms of F</u>
$V_0$	0.500	$2pq$	$(1 + 0.00)V_0, F = 0.00$
$V_1$	0.750	$3pq$	$(1 + 0.50)V_0, F = 0.50$
$V_2$	0.875	$3.5pq$	$(1 + 0.75)V_0, F = 0.75$
$V_\infty$	1.000	$4pq$	$(1 + 1.00)V_0, F = 1.00$

Genetic variances for dominance and overdominance gene actions can also be calculated similarly but with different codings. If complete dominance is assumed, AA, Aa, and aa are coded 2, 2, 0 and if overdominance is assumed, Aa has a larger value than AA.

The formula for additive variance in a random mating population is,

$$V_A = 2pq[a + d(q - p)]^2$$

where  $2a$  is the additive effect and  $d$  is the dominance effect at a locus.

The variance due to dominance is,

$$V_D = (2pqd)^2 \text{ (Falconer 1960).}$$

Horner et al. (1969) showed the fractions of the genetic variance

among selfed progeny means that are due to additive and dominance gene effects to be,

$$2pq(1 + F) \left[ a + \frac{1}{2}d(q - p) \left( \frac{1 - F}{1 + F} \right) \right]^2 \quad \text{and}$$

$$pq(p + Fq) (q + Fp) \left( \frac{1 - F}{1 + F} \right) d^2, \quad \text{respectively}$$

where  $F$  is the inbreeding coefficient of the parental plant and the rest are the same as before. They used  $\frac{1}{2}d$  instead of  $d$  for the  $Aa$  genotype since they were interested in the progeny means rather than individual plants. They stated that the variance among selfed progeny means that is due to additive gene effects is large compared with that due to dominance effects. As the generation of selfing increases, the frequency of heterozygotes decreases and the fraction of the genotypic variance that is due to dominance decreases regardless of the level of  $d$ .

#### Selection Based on Testcross Performance

Selection based on testcross performance largely depends on the amount of variance among testcross means. Horner et al. (1969) used the following formula, similar to that of Rawlings and Thompson (1962), to estimate the genetic variance in a two allele system.

$$V = 0.5pq(1 + F) [a + d(Q - P)]^2$$

where  $P$  and  $Q$  are the frequencies of  $A$  and  $a$ , respectively, in the tester and the other symbols are the same as before. They stated that if  $S_0$  plants or  $S_1$  lines are tested,  $F = 0.0$ . If  $S_1$  plants, which are equivalent to  $S_2$  lines, are tested,  $F = 0.5$ . In the absence of epistasis, the total variance is the sum over all loci. The expression shows that the variance of testcross means is a function of the additive effect of a gene or the

average effect of a gene substitution  $[a + d(Q - P)]$ , gene frequency in both the tested and the tester populations, and inbreeding of the tested plants. If a further assumption is made that A is also the favorable allele over a in the tester, the theoretical effectiveness of a tester can be visualized.

1. When  $d = 0$ , selection for high performance of the individuals of the population being tested will not be influenced by gene frequency of a tester, because  $d(Q - P) = 0$  in the expression.
2. When  $\underline{d} < 1.0$ , selection for high performance of the individuals of the population being tested favors AA genotypes. If the population being tested has a low frequency of AA genotypes, the rate of improvement will be large when Q is large.
3. When  $\underline{d} = 1.0$ , selection for high performance is ineffective if  $P = 1.0$ , because, in such circumstances, selection by testcross performance will not discriminate between individuals of the population tested, since  $AA = Aa$ . However, as the frequency of P gets smaller, more individuals with aa genotypes will be discarded, because a gametes of the tester are likely to unite with a of the population tested.
4. When  $\underline{d} > 1.0$  and  $P = 1.0$ , selection will favor aa genotypes. Aa genotypes will also be selected but less frequently, because a gametes from Aa genotypes can unite with the tester gamete. AA genotypes, however, will be discarded. As P decreases, selection for AA individuals increases and at  $P = 0.5$  the frequency of selecting each genotype will be the same since either A or a gametes of the tester will only show overdominance when united with a and A gametes of the population tested, respectively.

Horner et al. (1969) presented a very descriptive figure showing a comparison of the expected genotypic variances that are due to additive effects for selfed progenies and for testcross progenies based on the expressions shown for selfing and testcross progeny methods. In this model, the parental population was used as a tester. Their figure showed that the expected additive variance among the selfed progenies is much larger than among testcross progenies. Up to  $p = 0.2$ , the expected variance is similar for  $S_1$  and  $S_2$  progenies, but very low for testcross progenies. At  $p > 0.2$ ,  $S_2$  progenies show the greatest variation and testcross progenies the least variation. At  $p = 0.7$ , variance among  $S_2$  progeny means would be 14 times larger than among testcross progenies, and variance among  $S_1$  progeny means would be about four times larger than testcross progenies at  $p = 0.5$ . This shows that  $S_2$  progenies provide more opportunity for selection than both  $S_1$  and testcross progenies while testcross progenies provide the least opportunity.

#### Reciprocal Recurrent Selection

RRS has remained an effective method for improving two populations for combining ability with each other simultaneously at all levels of dominance. It was designed for characters that exhibit very low heritabilities and high heterosis. Comstock et al. (1949), who proposed the method, compared theoretical limits of improvement using RS for SCA and GCA, and RRS and concluded that:

1. When  $\underline{d} < 1.0$ , the improvement limit is the same for RS for GCA and RRS, but lower for SCA. The superiority of Aa genotype declines as the value of  $\underline{d}$  is reduced, and so RS for SCA will be less effective.

2. When  $d = 1.0$ , RS for GCA, SCA, and RRS will be equally effective. If the broad base tester is homozygous dominant for many favorable alleles, selection for GCA will be less efficient, because all testcross genotypes would have the same value.
3. When  $d > 1.0$ , RS for SCA and RRS will be the same, but RS for GCA will be inferior to both methods, because the mean of the individuals selected based on performance with the broad base tester is the average of all genotypes which would result in low response relative to the other two methods.

Cress (1966a) compared RRS with within population selection (WPS) based on theoretical considerations. WPS is the average response of the two populations, X and Y, for selection within populations (similar to RS for GCA). The rate of progress was measured by,

$$C = M_{xy} M_{yx} - \frac{1}{2}(M_{xx} M_{xx} + M_{yy} M_{yy})$$

where C is the difference which is the comparison of the rate of improvement between RRS and WPS,

$M_{xy} M_{yx}$  is the mating system for RRS, and

$M_{xx} M_{xx}$  and  $M_{yy} M_{yy}$  are mating systems within population X and Y,

respectively.

If A is the favorable gene over its allele, a, in both populations, and p and P are the gene frequencies for favorable allele in the X and Y populations, respectively, the theoretical rate of improvement is:

1. When  $(p + P) < 1.0$ , RRS is better than WPS for all positive dominance.
2. When  $(p + P) > 1.0$ , WPS is faster in the rate of the improvement than RRS for levels of dominance including complete dominance because the larger proportion of the favorable alleles contributes

larger additive variance with the WPS method.

3. If overdominance is present, RRS is better when  $(p + P) > 1.0$  and the difference between  $p$  and  $P$  must be large enough to see pronounced result. If  $p = P$ ,  $RRS = WPS$ , and the rate of progress in RRS is dependent on the additive variance in the testcrosses.

Cress (1967), using the simulation method, also compared RRS as proposed by Comstock et al. (1949),  $RRS_S$ , modified by additional selfing prior to testcrossing, and  $RRS_C$ , using the original parents as testers over 30 cycles. Generally, the results showed that RRS and  $RRS_S$  methods provided high and linear mean response in hybrid combinations between populations at all level of dominance with  $RRS_S$  being superior over RRS in the rate of progress in early cycles.

#### Comparisons of $S_1$ , $S_2$ , and Half-Sib Methods

Selfed and half-sib progeny selection methods have been compared more frequently since the early 1960's, but the question as to which method is most effective still remains unanswered. The first attempt was made by Davis (1934) in which he compared selfed lines and their crosses with an unrelated open-pollinated variety tester. He indicated that average yield of the first and second inbred generations was important for selection. Genter and Alexander (1962) made a comparative performance test between  $S_1$  progenies and progenies selected on the basis of testcross performance with single cross testers. They found more dispersed means and less environmental effects from  $S_1$  progenies than from testcrosses. Koble and Rinke (1963), Lonquist and Lindsey (1964), Torregroza and Harpstead (1965), and Lonquist and Castro (1967) all made similar reports

that the  $S_1$  progeny method was more effective for selection than testcross methods with related and unrelated testers. Duclos (1967) and Duclos and Crane (1968), however, found no significant difference between  $S_1$  progeny and topcross methods.

Comparisons of advanced populations developed by different methods of recurrent selection have been made in order to evaluate the effectiveness of the methods. Genter (1966) found mean yield increases of 31% and 18% with two cycles of  $S_1$  and testcross selection, respectively. In 1973, he obtained a population yield of 9.0 q/ha (11%) more from the second cycle of  $S_1$  selection than from the testcross populations. However, Genter and Eberhart (1974) obtained the same yield response from both VCBS(S) $C_4$  and VCBS(HT) $C_3$  developed from Virginia Corn Belt-Southern Synthetic by four cycles of RS for  $S_1$  progeny yield and by three cycles of half-sib selection, respectively. BSK(S) $C_4$ , developed from Krug Hi syn-1 by four cycles of  $S_1$  selection, and BSSS(HT) $C_7$ , developed from 'Stiff Stalk Synthetic' by seven cycles of half-sib selection, failed to show any improvement. Carangal (1967) stated that RS on the basis of  $S_1$  and topcross evaluation was effective in both cases in increasing the frequency of favorable genes for yield in synthetic A. However,  $S_1$  evaluation showed greater improvement in the first cycle synthetic made from the selected lines. Later, Carangal et al. (1971) indicated that  $S_1$  progeny evaluation was more efficient than testcross evaluation even for GCA. Burton et al. (1971), using a double cross tester, obtained about 6% yield increase from the testcross series, but 16% from the selfing series for yield of populations per se. Combining ability with four testers was also improved more by the  $S_1$  method.

Horner (1963) compared  $S_1$  lines and  $S_1$  plants (which are equivalent to  $S_2$  lines) and stated that selection for combining ability can be done more effectively among individual  $S_1$  plants than among  $S_0$  plants or  $S_1$  lines. The variance component estimate for crosses involving  $S_1$  plants was larger than for crosses of  $S_1$  lines. This shows that subsequent selfings do provide an opportunity for more effective selection. Horner et al. (1969) found that the  $S_2$  progeny method was as effective as the parental tester method for population improvement and suggested that it places more emphasis on contribution of homozygous loci than heterozygous loci, whereas the parental tester method emphasizes the contribution of heterozygous loci to a greater extent, resulting in a higher yielding syn-3 population. In 1973, from two additional cycles, they reported a gain in GCA of 4.4% per cycle from an inbred tester method compared with 2.4% and 2% for the parental and  $S_2$  progeny methods, respectively.

RRS, regardless of the type of gene action involved, theoretically is considered effective in producing lines with SCA for yield and vigor between two populations. Thomas and Grissom (1961) evaluated RRS for popping volume, grain yield, and resistance to root lodging in popcorn and concluded that RRS was effective in improving the mean of the two populations simultaneously. However, nearly the same improvements were made when  $S_4$  lines were developed from direct selfing in the two populations. Moll and Stuber (1971) compared full-sib family selection and RRS for higher grain yield in the varieties 'Jarvis' and 'Indian Chief' following six cycles of selection, and stated that heterosis in the variety hybrid increased about 30% more after RRS than after full-sib family selection within each population.

Darrah et al. (1972) obtained an 8 q/h<sub>a</sub> larger gain in yield from RRS compared with modified ear-to-row method in variety H611, but there was no significant difference between methods in varieties K11 and Ec573. Russel and Eberhart (1975) evaluated three crosses among BSCB(R)<sub>C<sub>5</sub></sub>, BSSS(R)<sub>C<sub>5</sub></sub>, and BSSS(HT)<sub>C<sub>6</sub></sub> populations improved by five cycles of RRS and six cycles of testcross selection with a double-cross than from the population crosses. There was no significant difference among the population crosses. Robinson (1976) obtained a higher estimate of genetic variance from S<sub>2</sub> line evaluation than from half-sib progeny evaluation in the initial cycle of a selection program comparing the RRS and S<sub>2</sub> progeny methods.

## MATERIALS AND METHODS

### Sources of Materials

The  $S_2$  lines used in this study were derived from Populations A and B of FSHMR, a synthetic variety developed recently by the Florida Agricultural Experiment Stations for resistance to the fungus Helminthosporium maydis N. and M. These lines had been evaluated by Robinson (1976) for combining ability with an  $S_1$  line tester and performance of  $S_2$  lines per se. The testers used were a line (Tester A) from Population A to evaluate lines from Population B and a line (Tester B) from Population B to evaluate lines from Population A.

### Crosses Made to Compare Methods

On the basis of data obtained by Robinson (1976), eight groups of 10 lines each were chosen as follows:

1. AHT - High yielding Population A lines (Testcross data)
2. ALT - Low yielding Population A lines (Testcross data)
3. AHS<sub>2</sub> - High yielding Population A lines ( $S_2$  line data)
4. ALS<sub>2</sub> - Low yielding Population A lines ( $S_2$  line data)
5. BHT - High yielding Population B lines (Testcross data)
6. BLT - Low yielding Population B lines (Testcross data)

7. BHS<sub>2</sub> - High yielding Population B lines (S<sub>2</sub> line data)

8. BLS<sub>2</sub> - Low yielding Population B lines (S<sub>2</sub> line data)

The individual lines making up the above groups and their performance data either in testcrosses or as S<sub>2</sub> progenies per se are shown in Table 1. In addition, a similar series of eight six-line groups were established with the limitation that the lines within groups would not be related to each other according to pedigree records. These lines and their performance records are listed in Table 2. Some lines not listed in Table 1 had to be used in the second series to avoid inclusion of related lines. This resulted in slightly lower mean performances of the groups in Table 2 than in Table 1.

All of the lines listed in Table 1 and 2, together with Tester A, Tester B, and the doublecrosses Coker 71 and Greenwood 471, were grown near Homestead, Florida during the Winter of 1975-1976 in sufficient quantities to make the following crosses using standard controlled-pollination techniques: For lines in Table 1, (a) each line was crossed with Coker 71 and Greenwood 471, using one plant of each hybrid as the female parent, (b) each line from Population A was crossed with Tester B and each line from Population B was crossed with Tester A, using two plants of each line as the female parents, and (c) interpopulation crosses between A and B populations within breeding methods were made. AHT x BHT, ALT x BLT, AHS<sub>2</sub> x BHS<sub>2</sub>, ALS<sub>2</sub> x BLS<sub>2</sub>, AHT x BLT, BHT x ALT, AHS<sub>2</sub> x BLS<sub>2</sub>, and BHS<sub>2</sub> x ALS<sub>2</sub>. For each cross one group was designated the female parent. Two or three ears of each female line was pollinated by pollen from each line in the male group. For lines in Table 2, all possible intra-group crosses were made, including reciprocals, to produce first generation synthetics of the eight groups.

Table 1  
Lines Used in Testcross Evaluations.

Population	High testcross (HT)		Low testcross (LT)		High inbred (HS) <sub>2</sub>		Low inbred (LS) <sub>2</sub>	
	Line No.	Grain yield	Line No.	Grain yield	Line No.	Grain yield	Line No.	Grain yield
Population A		kg/ha		kg/ha		kg/ha		kg/ha
	42448-1	4972	42421-2	3737	42430-1	3642	42421-2	1436
	42452-1	4998	42491-1	3429	42435-2	3222	42436-4	1350
	42453-1	4855	42493-1	3627	42453-2	2995	42446-3	1400
	42454-1	5211	42543-1	3180	42454-1	3286	42463-2	999
	42456-1	5192	42544-1	3402	42456-1	2996	42463-3	1061
	42456-2	5114	42545-1	3558	42456-2	3231	42466-2	1290
	42459-1	5103	42613-2	3561	42459-1	3203	42490-3	1072
	42471-1	4824	42674-1	3646	42462-3	3151	42589-1	1478
	42472-3	5129	42743-1	3652	42735-1	3073	42612-3	584
	42605-2	4768	42823-1	3488	42762-1	3108	42613-2	817
	Mean	5017		3528		3191		1149
Population B								
	42395-3	5165	41968-1	3975	42415-2	2728	42443-4	1190
	42415-1	5550	41990-1	4078	42418-2	3696	42444-2	815
	42415-4	5535	42408-1	4190	42562-3	2778	42415-3	1160
	42570-1	5359	42441-1	4188	42570-1	2828	42564-3	1053
	42574-3	5292	42443-4	4144	42572-1	2716	42631-2	754
	42631-3	5110	42443-6	4071	42607-1	2716	42631-3	1275
	42685-1	5087	42549-1	4168	42710-1	2627	42650-1	1297
	42706-1	5418	42563-3	4209	42697-1	2867	42657-1	1281
	42752-2	5333	42795-1	4217	42697-2	2829	42678-1	1125
	42772-3	5332	42816-1	4210	42715-1	3569	42686-2	1049
	Mean	5318		4145		2935		1100

Table 2  
Lines Used in Evaluation of Synthetics.

Population	High testcross		Low testcross		High inbred		Low inbred	
	Line No.	Grain yield kg/ha	Line No.	Grain yield kg/ha	Line No.	Grain yield kg/ha	Line No.	Grain yield kg/ha
Population A	42456-1	5192	42421-2	3737	42435-2	3222	42421-2	1436
	42461-1	4838	42491-1	3429	42454-1	3286	42446-3	1400
	42472-3	5129	42543-1	3180	42550-1	2803	42466-2	1290
	42550-1	4613	42613-2	3561	42605-2	2834	42478-1	1546
	42605-2	4768	42743-1	3652	42735-1	3073	42490-3	1072
	42765-3	4736	42823-1	3488	42762-1	3108	42613-2	817
	Mean	4879		3508		3054		1260
Population B	42415-1	5550	41968-1	3975	42415-2	2728	42424-2	815
	42631-3	5110	41990-1	4078	42570-1	2828	42631-2	754
	42680-2	4970	42408-1	4190	42607-1	2716	42650-1	1297
	42685-1	5087	42441-1	4188	42710-1	2627	42657-1	1281
	42752-2	5333	42795-1	4217	42715-1	3569	42678-1	1225
	42772-3	5332	42816-1	4210	42813-1	2515	42686-2	1049
	Mean	5230		4143		2830		1053

When the seeds were mature the ears were harvested and taken to Gainesville for drying and shelling. After sorting according to group and type of cross, composites were made by mixing approximately equal numbers of seed from each individual cross within the various group x tester, population x population, and intra-group combinations. A total of 40 such composites were prepared (24 group x tester, eight synthetics, and eight population x population).

### Experimental Designs

The 40 composites described above were evaluated in two-row plots at two locations, the Agronomy Farm adjacent to the University of Florida Campus in Gainesville and the Agronomy Green Acres Farm 12 miles west of Gainesville. Row spacing was 90 cm and the plants were spaced 30 cm apart in the rows. Two seeds were planted per hill and the plants were thinned to one per hill when they reached 15 cm height. Thirty plants per plot were used on the Campus Farm and 26 plants on the Green Acres Farm. Missing hills were replanted with a purple-stalk hybrid to provide uniform competition to all plants.

A split-plot experimental design was used to evaluate the testcrosses, with the three testers as main plots and the four selected groups of a population (A or B) as subplots. Separate experiments were conducted for the A and B populations. The main plots were assigned to each block at random and the subplots were randomized within main plots. Ten replications were used at each location.

The four synthetics from each population were also evaluated in separate experiments. A randomized complete block design was used with

15 replications at each location.

The eight interpopulation crosses were tested in a randomized complete block experiment with 10 replications at each location.

The plots at both locations received uniform applications of fertilizer and pesticides, and were irrigated when necessary to prevent excessive drought stress. Additional nitrogen was applied at the Green Acres location about 6 weeks after planting when pronounced deficiency symptoms developed.

#### Data Collection

Prior to data collection, deformed and purple-stalked plants were discarded from the field. Plants badly damaged by smut were also removed from the Green Acres field. Data on total number of plants, average ear height, husk score, and lodging were taken from every plot. Ear height was taken on a plant that represented the average ear height in the plot; the measurement was made from ground level to the node of attachment of the ear. A husk score for each plot was determined on one to nine rating scale, one being best with relatively tight husk and well-covered ears and nine lacking such characteristics. Root lodging was also taken on a one to nine rating scale where one was assigned to a plot with less than 10% of the plants lodged and nine with greater than 90% of the plants lodged.

At harvest, data on number of plants erect, ear quality score, total number of ears, and number of ears rotten were recorded. Yield per plot was taken by weighing the ears to the nearest 0.1 pound (45g). Finally, yield was adjusted to full stand by multiplying the yield at harvest by

the ratio of the number of plants at full stand to the number of plants harvested corrected by an adjustment factor. The factors used for each missing plant were 0.75 for Green Acres and 0.50 for Gainesville. The factors were chosen to minimize yield advantage that a plot with a poor stand might have compared with those plots with full stand, since plants in a plot with a poor stand have less competition for light and soil nutrients.

### Statistical Procedure

Since our primary interest at this stage was on the yield performance of the groups, analysis of variance (AOV) was made for the adjusted yield only. For the other characteristics measured, means were calculated.

AOV for the testcrosses was based on the model,

$$X_{ijk\ell mn} = \mu + A_i + B_j(i) + T_k + AT_{ik} + E_{\ell}(ijk) + S_m + AS_{im} + TS_{km} + ATS_{ikm} + E_n(ijkm)$$

where  $\mu$  is the overall mean

$A_i$  is the effect of the  $i$ th location,  $i = 1, 2$

$B_j(i)$  is the effect of the  $j$ th block in the  $i$ th location,  $j = 1, \dots, 20$

$T_k$  is the effect of the  $k$ th tester,  $k = 1, 2, 3$

$AT_{ik}$  is the interaction effect of the  $i$ th location and the  $k$ th tester

$E_{\ell}(ijk)$  is the error term of the  $\ell$ th unit in  $i$ th location,  $j$ th block, and  $k$ th tester

$S_m$  is the treatment effect of the  $m$ th group,  $m = 1, 2, 3, 4$

$AS_{im}$  is the interaction effect of the  $i$ th location and the  $m$ th group

$TS_{km}$  is the interaction effect of the  $k$ th tester and the  $m$ th group

$ATS_{ikm}$  is the interaction effect of the  $i$ th location,  $k$ th tester, and  $m$ th group

$E_{n(ijkm)}$  is the error term of the  $n$ th sub-unit in the  $i$ th location,  $j$ th block,  $k$ th tester, and  $m$ th treatment.

The combined AOV for the adjusted yield of testcrosses was done as follows:

Sources	Df	SS	MS
Locations	$l - 1$	$SS_1$	$MS_1$
Blocks/Ls	$(r_1 - 1) + (r_2 - 1)$	$SS_2$	$MS_2$
Testers	$a - 1$	$SS_3$	$MS_3$
L x T	$(l - 1) (a - 1)$	$SS_4$	$MS_4$
Error (A)	$[(r_1 - 1) + (r_2 - 1)] \times (a - 1)$	$SS_5$	$MS_5$
Groups	$b - 1$	$SS_6$	$MS_6$
L x G	$(l - 1) (b - 1)$	$SS_7$	$MS_7$
T x G	$(a - 1) (b - 1)$	$SS_8$	$MS_8$
L x T x G	$(l - 1) (a - 1) (b - 1)$	$SS_9$	$MS_9$
Error (B)	$a[(r_1 - 1) + (r_2 - 1)] \times (b - 1)$	$SS_{10}$	$MS_{10}$

AOV for the synthetics or the interpopulation hybrids were based on the model,

$$X_{ijk\ell} = \mu + A_i + B_j + S_k + AS_{ik} + E_{l(ijk)}$$

where  $\mu$  is the overall mean

$A_i$  is the effect of the  $i$ th location,  $i = 1, 2$

$B_j$  is the effect of the  $j$ th block in the  $i$ th location

$j = 1, \dots, 30$  for the synthetics

$j = 1, \dots, 20$  for the hybrids

$S_k$  is the effect of the  $k$ th treatment

$k = 1, 2, 3, 4$  for the synthetics

$k = 1, \dots, 8$  for the hybrids

$AS_{ik}$  is the interaction effect of the  $i$ th location and  $k$ th treatment

$E_{l(ijk)}$  is the error term of the  $l$ th unit in the  $i$ th location,  $j$ th block, and  $k$ th treatment. All factors except the blocks are fixed.

The combined AOV for the adjusted yield was as follows:

Sources	Df	SS	MS
Locations (L)	$l - 1$	$SS_1$	$MS_1$
Blocks/Ls	$(r_1 - 1) + (r_2 - 1)$	$SS_2$	$MS_2$
Treatments (T)	$t - 1$	$SS_3$	$MS_3$
L x T	$(l - 1) (t - 1)$	$SS_4$	$MS_4$
Error	$[(r_1 - 1) + (r_2 - 1)] \times (t - 1)$	$SS_5$	$MS_5$

The two breeding methods were compared using Duncan's new multiple-range test and single degree of freedom contrast following the procedure shown in Steel and Torrie, 1960.

## RESULTS

### Testcrosses

Mean squares and F ratios from the analysis of testcross yield data involving four selected groups of inbred lines from each population in crosses with three testers are shown in Table 3. In both populations there were highly significant differences among groups averaged over testers, and the tester x group interaction was significant at the 0.05 level in Population A and at the 0.01 level in Population B. The tester x location interaction was highly significant in Population B but not in A.

Means for yield of individual group x tester combinations and for groups over testers are shown in Table 4. The crosses involving HT groups were not significantly different from those involving HS<sub>2</sub> groups for all testers except Coker 71 in Population A or for means over testers. In contrast, the LT crosses were significantly lower in combining ability on the average than the LS<sub>2</sub> crosses and there was a significantly larger difference in average combining ability between HT and LT than between HS<sub>2</sub> and LS<sub>2</sub> in both populations.

The interaction of testers with groups in Population A was due primarily to the fact that HS<sub>2</sub> and LS<sub>2</sub> combined more poorly with Coker 71 and better with Greenwood 471 than would be expected on the basis of the other tester x group yields. In Population B, the significant

Table 3  
Mean Squares and F Ratios for Testcrosses.

Sources of variation	Df	Population A		Population B	
		Mean square	F ratio	Mean square	F ratio
Main plots					
Locations (L)	1	169.780	43.9389 <sup>***</sup>	308.205	195.6857 <sup>***</sup>
Blocks/Locations	18	3.864	3.8640 <sup>***</sup>	1.575	3.3298 <sup>***</sup>
Testers (T)	2	2.384	2.3840	0.815	1.7230
T x L	2	1.004	1.0040	3.418	7.2262 <sup>***</sup>
Error (a)	36	1.000		0.473	
Sub-plots					
Groups (G)	3	5.385	14.2084 <sup>***</sup>	3.713	15.6008 <sup>***</sup>
L x G	3	0.565	1.4907	0.382	1.6050
T x G	6	0.864	2.2797 <sup>*</sup>	0.755	3.1723 <sup>***</sup>
L x T x G	6	0.775	2.0448	0.193	0.8109
Error (b)	162	0.379		0.238	
Total	239				

<sup>\*\*\*</sup> Significant at the 0.01 level.

<sup>\*</sup> Significant at the 0.05 level.

Table 4  
 Mean Performance for Testcrosses of Lines Selected  
 for High and Low Yield by Two Methods.

Selected group	Tester			Average
	Inbred tester	Coker 71	Greenwood 471	
	kg/ha			
Population A				
HT	5067a*	5306a	5136a	5170a
LT	4188c	4715b	4703b	4535c
HS <sub>2</sub>	4982a	4886b	5301a	5056a
LS <sub>2</sub>	4637b	4564b	5124a	4775b
Population B				
HT	5312a	5167a	5041a	5173a
LT	4548b	4734b	4618b	4633c
HS <sub>2</sub>	5038a	5176a	5070a	5095ab
LS <sub>2</sub>	4540b	5220a	5020a	4927b

\* Means in columns within populations followed by different letters are significantly different at the 0.05 level according to Duncan's New Multiple-range Test.

tester x group interaction was caused mostly by the failure of the two double-cross testers to differentiate among the HT, HS<sub>2</sub>, and LS<sub>2</sub> groups, while the inbred tester combined significantly more poorly with LS<sub>2</sub> than with HS<sub>2</sub>.

### Synthetics

Mean squares and F ratios from the analyses of yield data involving synthetics from the four selected groups of inbred lines from each population are presented in Table 5. In both populations, differences among groups were highly significant. The highly significant synthetics by locations interaction in Population B was due to the fact that the HS<sub>2</sub> and LS<sub>2</sub> synthetics did not yield as well at Green Acres as they did at Gainesville relative to the HT and LT synthetics (Figure 1).

Means for yield of the four synthetics from each population are shown in Table 6. The yield of the HT synthetic was not significantly different from the HS<sub>2</sub> synthetic and likewise the LT synthetic was not significantly different from the LS<sub>2</sub> synthetic within populations. However, the high and low synthetics within populations were significantly different at the 0.01 level for each method of selection.

To obtain measures of repeatability for combining ability with the two inbred testers used by Robinson (1976) and to estimate heritability with both methods of selection, differences between means of high and low selections in 1975 were compared with the 1976 evaluations of the various selected groups. The upper half of Table 7 shows comparisons of the two methods provided by crosses of selected groups with the two inbred testers, and the lower half shows comparisons by use of synthetics

Table 5  
Mean Squares and F Ratios for Synthetics.

Sources of variation	Df	Population A		Population B	
		Mean square	F ratio	Mean square	F ratio
Locations (L)	1	113.294	271.6882 <sup>**</sup>	101.875	156.4900 <sup>**</sup>
Blocks/Locations	28	0.417	1.2991	0.651	2.3759 <sup>**</sup>
Synthetics (S)	3	4.515	14.0654 <sup>**</sup>	3.987	14.5511 <sup>**</sup>
S x L	3	0.101	0.3146	1.227	4.4781 <sup>**</sup>
Error	84	0.321		0.274	
Total	119				

\*\* Significant at the 0.01 level.

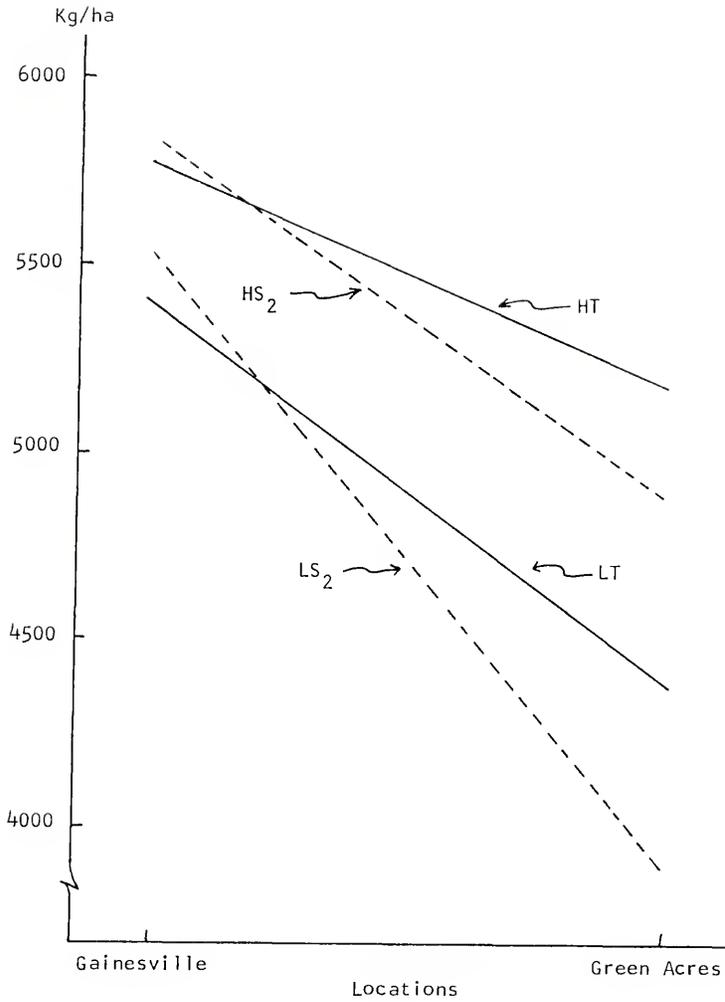


Figure 1  
Population B Synthetics by Location Interactions.

Table 6  
Grain Yield Performance of Synthetics of Lines Selected  
for High and Low Yield.

Method of evaluation	Population A	Population B
	————— kg/ha —————	
Synthetics		
HT	4963a*	5477a
LT	4458b	4891b
HS <sub>2</sub>	5003a	5360a
LS <sub>2</sub>	4240b	4717b

\* Means within columns followed by different letters are significantly different at the 0.01 level.

Table 7  
 Mean Grain Yield of Selected Groups in 1975 and 1976 and Ratios of Differences  
 Between High and Low Means in the Two Years.

Methods of selection	Population A			Population B		
	Mean yield of selected lines 1975 <sup>#</sup>	Yield in 1976 evaluation	Ratio 1976 H - L / 1975 H - L	Mean yield of selected lines 1975	Yield in 1976 evaluation	Ratio 1976 H - L / 1975 H - L
	kg/ha					
	Line x Tester B Group x Tester B			Line x Tester A Group x Tester A		
	<u>Means</u>			<u>Means</u>		
HT	5071	5067 <sup>a</sup>		5318	5312 <sup>a</sup>	
LT	3528	4188 <sup>b</sup>		4145	4548 <sup>b</sup>	
Difference	1489	879	0.59	1173	764	0.65
HS2	3191	4982 <sup>a</sup>		2935	5038 <sup>a</sup>	
LS2	1149	4637 <sup>a</sup>		1100	4540 <sup>b</sup>	
Difference	2042	345	0.17	1835	498	0.27
	Line x Tester B Synthetics			Line x Tester A Synthetics		
	<u>Means</u>			<u>Means</u>		
HT	4879	4963 <sup>a</sup>		5230	5477 <sup>a</sup>	
LT	3508	4458 <sup>b</sup>		4143	4891 <sup>b</sup>	
Difference	1371	505	0.36	1087	586	0.54
HS2	3054	5003 <sup>a</sup>		2830	5360 <sup>a</sup>	
LS2	1260	4240 <sup>b</sup>		1053	4717 <sup>b</sup>	
Difference	1794	763	0.42	1777	643	0.36

\* Data collected by Robinson (1976) and used to select high and low groups.

# Means in columns within evaluations followed by different letters are significantly different at the 0.05 level.

developed from each selected group. Repeatability of combining ability with the same tester in the two years was 59% in Population A and 65% in Population B (ratios of 0.59 and 0.65, respectively, of high-low in 1976 to high-low in 1975). When selection was based on  $S_2$  progeny performance and the 1976 evaluation was for combining ability with the inbred testers, realized "heritability" was only 17% in Population A and 27% in Population B (ratios of 0.17 and 0.27). When evaluation was done by producing synthetics, the Inbred Tester Method resulted in ratios of 0.36 and 0.54 and the  $S_2$  Progeny Method in ratios of 0.42 and 0.46 for Populations A and B, respectively. These results indicate that the two methods were equally effective with respect to yield of synthetics.

#### Interpopulation Crosses

Mean squares and F ratios from the analysis of yield data of eight interpopulation crosses are shown in Table 8. Yield differences among crosses were highly significant (Table 9). The High x High crosses were significantly higher yielding than the Low x Low crosses with both methods, and the average of the two High x Low crosses for each method was not significantly different from the average of the High x High and Low x Low crosses as shown in Figure 2.

#### Summary of Evaluation Methods

Differences in average performance between high and low groups of lines selected by the two methods for four methods of evaluation are summarized in Table 10. Larger yield differences were obtained from

Table 8  
 Mean Squares and F Ratios for Interpopulation Crosses.

Sources of variation	Df	Mean square	F ratio
Locations (L)	1	75.282	41.6844 <sup>***</sup>
Blocks/Locations	18	1.806	4.4373 <sup>**</sup>
Crosses (C)	7	1.757	4.3169 <sup>**</sup>
L x C	7	0.177	0.4349
Error	126	0.407	
Total	159		

<sup>\*\*\*</sup> Significant at the 0.01 level.

<sup>\*</sup> Significant at the 0.05 level.

Table 9  
Grain Yield Performance of Interpopulation Crosses  
of Lines Selected for High and Low Yield.

Cross	Grain yield
	kg/ha
AHT x BHT	5383 <sup>a*</sup>
AHT x BLT	5281 <sup>ab</sup>
Mean	5332
ALT x BHT	4830 <sup>cd</sup>
ALT x BLT	4689 <sup>d</sup>
Mean	4759.5
AHS <sub>2</sub> x BHS <sub>2</sub>	5529 <sup>a</sup>
AHS <sub>2</sub> x BLS <sub>2</sub>	5111 <sup>abc</sup>
Mean	5320
ALS <sub>2</sub> x BHS <sub>2</sub>	4948 <sup>bcd</sup>
ALS <sub>2</sub> x BLS <sub>2</sub>	4937 <sup>bcd</sup>
Mean	4942.5

\* Means followed by different letters are significantly different at the 0.05 level.

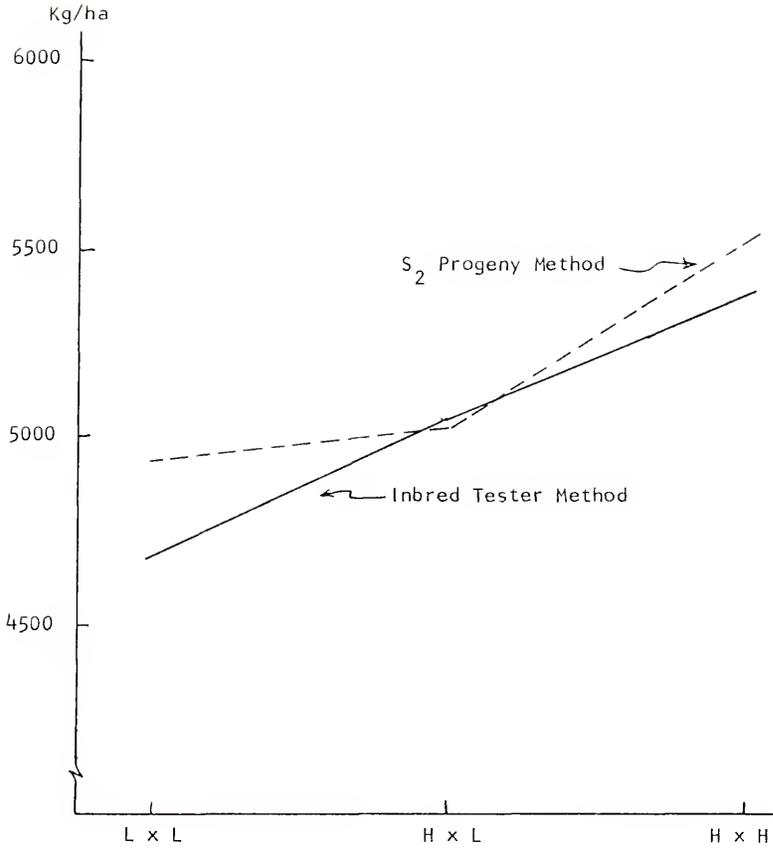


Figure 2  
Average Yield of Interpopulation Crosses of High and Low Yielding Lines by the Two Methods.

Table 10  
Differences in Grain Yield Between High and Low  
Groups when Evaluated by Four Methods.

Methods of evaluation	Inbred Tester Method		S <sub>2</sub> Progeny Method	
	Population A	Population B	Population A	Population B
Inbred tester	879	764	345	498
Ave. of double		821		421
cross testers	512	428	249	3
Synthetics	505	568	763	643
Interpopulation				703
crosses	572	121	377	214
Mean	617	475	433	339
		545		386

kg/ha

group x inbred testers evaluation of lines selected from Populations A and B by the Inbred Tester Method compared with lines selected by  $S_2$  Progeny Method. On the other hand, larger differences were obtained between synthetics developed from lines selected by the  $S_2$  Progeny Method compared with lines selected by the Inbred Tester Method. Yield differences between groups for combining ability with two double-crosses were larger for lines selected by the Inbred Tester Method than for lines selected by the  $S_2$  Progeny Method. Results of interpopulation crosses indicated that the two methods were similar. For the average over all evaluation methods, the Inbred Tester Method showed relatively greater yield differences between high and low selections than the  $S_2$  Progeny Method.

#### Characteristics Other than Yield

Differences in response between high and low groups for other characteristics and their averages over the four methods of evaluation are shown in Table 11. The groups were selected primarily for high and low yield. Numbers preceded by negative signs show that selections for low yield were associated with higher mean responses for the characteristic measured than the corresponding high yield group. Positive ear weight and negative ear height differences were shown for all evaluations of the lines selected by the Inbred Tester Method in both populations. In contrast, positive differences for ears per plant were shown for all evaluations of the lines selected by the  $S_2$  Progeny Method in both populations. On the average over the two populations, ear weight difference was much greater for groups selected by the

Table 11  
Differences in Response for Characteristics other than Yield  
Between High and Low Groups Selected by Two Methods

Methods of evaluation	Characteristics							
	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect
	g		cm			%		%
<u>Inbred Tester Method</u>								
Population A								
Inbred Tester B	27.00	0.01	-3.0*	0.55	-0.05	0.004	-0.15	0.00
Avg. double								
cross testers	3.00	0.10	-3.0	-0.30	0.18	-0.010	-0.20	-0.02
Synthetics	18.00	-0.05	-2.0	1.30	0.16	-0.010	0.04	-0.04
Interpopulation								
crosses	7.00	0.09	-3.5	0.70	0.50	-0.004	-0.22	0.00
Average	13.75	0.04	-2.9	0.56	0.20	-0.005	-0.13	-0.01
Population B								
Inbred Tester A	22.00	0.03	-7.0	0.60	-0.05	-0.010	-0.15	0.07
Avg. double								
cross testers	13.00	0.03	-2.0	-0.57	-0.07	0.010	-0.10	0.02
Synthetics	22.00	0.01	-4.0	-1.63	-0.66	-0.010	0.02	0.07
Interpopulation								
crosses	16.00	-0.05	-0.5	-0.95	-0.35	0.004	-0.22	0.03
Average	18.25	0.00	-3.4	-0.64	-0.28	-0.001	-0.11	0.05
<u>S<sub>2</sub> Progeny Method</u>								
Population A								
Inbred Tester B	9.00	0.03	3.0	0.95	0.10	-0.001	-0.05	0.01
Avg. double								
cross testers	-5.00	0.07	-3.0	0.30	0.10	0.003	-0.07	0.03
Synthetics	13.00	0.06	-1.0	-0.07	0.30	-0.008	-0.07	-0.01
Interpopulation								
crosses	-7.00	0.14	-3.5	0.60	0.00	0.009	0.10	0.01
Average	2.50	0.07	-1.1	0.44	0.12	0.001	0.02	0.01
Population B								
Inbred Tester A	9.00	0.08	8.0	0.45	0.05	0.004	-0.05	0.02
Avg. double								
cross testers	2.00	0.00	1.0	0.62	-0.10	0.003	0.03	0.00
Synthetics	-13.00	0.16	-1.0	0.03	0.20	-0.004	-0.14	0.03
Interpopulation								
crosses	7.00	0.00	0.5	-0.20	-0.05	-0.004	0.15	0.03
Average	1.25	0.06	2.1	0.22	0.02	0.000	-0.08	0.02

\* Numbers preceded by negative signs show that the low groups exceed the high groups in measurement of the characteristics.

Inbred Tester Method than for groups selected by the  $S_2$  Progeny Method. Except for ear weight, ears per plant, and plants erect, average differences were negative for groups selected by the Inbred Tester Method whereas differences except for root lodging score were positive for groups selected by  $S_2$  Progeny Method.

## DISCUSSION

Although the Inbred Tester Method was more effective than the  $S_2$  Progeny Method for separating high and low combining ability groups, the two methods appeared to be equally effective for selecting high combining lines for grain yield. This is evident from the fact that the HT and  $HS_2$  groups in both populations were not significantly different in (1) combining ability with the two unrelated doublecross testers, (2) yield of synthetics developed from them, or (3) yield of HT x HT and  $HS_2$  x  $HS_2$  crosses between populations. These results indicate that the breeder should select lines that produce good grain yields as inbreds, which is very desirable from the hybrid seed production point of view. Selection for low yield with the  $S_2$  Progeny Method, on the other hand, did not result in significantly lower combining ability with unrelated doublecross testers than did selection for high yield of  $S_2$  lines. This suggests that low yield of some inbred lines may have been due to homozygosity for a few deleterious recessive genes rather than to a low frequency of dominant favorable genes over the entire genotype. In crosses with the doublecross testers, such deleterious genes probably were masked by dominant genes in the testers, resulting in higher than expected yields. When the Population A  $LS_2$  and Population B  $LS_2$  groups were crossed, yield of the hybrid was significantly lower than yield of the  $HS_2$  interpopulation cross. Also, synthetics produced by intercrossing lines within the two  $LS_2$  groups were significantly lower than

those from  $HS_2$  groups and were comparable to the LT synthetics. Apparently there was less masking of homozygous recessive deleterious genes in low x low combinations than in crosses between the  $LS_2$  groups and the doublecross testers.

The inbred testers were more effective than the doublecross testers in measuring differences in combining ability between selected high and low groups. As mentioned above, the doublecross testers showed no significant difference between the  $HS_2$  and  $LS_2$  groups in either population, but the inbred tester for each population indicated significant differences between these groups for combining ability. Data on the synthetics and intergroup crosses show conclusively that the  $HS_2$  and  $LS_2$  groups in each population differed in frequency of favorable genes. We can conclude, therefore, that heterogeneous, heterozygous testers such as the two commercial doublecrosses used in this study are ineffective for detecting small differences in combining ability. They were effective in showing significant differences between the HT and LT groups, however, where combining ability differences were larger than those between the  $HS_2$  and  $LS_2$  groups. These results are in agreement with those of Horner et al. (1973), who found that an inbred tester was about twice as effective as a heterozygous population for improving frequency of genes having additive effects. The crosses between the HT groups and the inbred testers had grain yields similar to the means of the same crosses when tested individually in 1975 by Robinson (1976). Differences between the high and low groups were 59 and 65% as large in 1976 as in 1975 for Population A and B, respectively. This level of repeatability of yield measurement in different years is good. A perfect correlation between the 1975 and 1976 results would not be

expected because experimental error and genotype x environment interaction cause variation in grain yield from year to year.

Estimates of realized heritability, based on yield of synthetics developed from the high and low groups, were rather low compared with the repeatability estimates. For the Inbred Tester Method, comparisons of differences between the high and low group means in 1975 and of the synthetics tested in 1976 indicate that heritability was 36 and 54%, respectively, for the A and B Populations. Comparable estimates for the  $S_2$  Progeny Method were 42 and 36%. These results show, however, that both methods were effective in differentiating among  $S_2$  lines for additive genetic differences that affect the yield of synthetics. There appears to be no significant difference between the two methods in this respect.

The yields of the high x high, high x low, and low x low inter-population crosses suggest that gene action for yield was predominantly additive. With each method of selection, mean yield of the high x low crosses was not significantly different from the mean of the high x high and low x low crosses. If dominance is of major importance and two alleles per locus are assumed, the high x low crosses would be expected to yield more than the mean of the high x high and low x low combinations. It is known, however, that dominance is very important to the yield of maize. In the populations studied here, Robinson (1976) found that the mean yield of  $S_2$  lines was only about 46% as much as mean yield of half-sib families. This degree of inbreeding depression can only be explained by a high level of dominance of favorable genes. It seems likely that multiple alleles were involved in these inter-population crosses between groups of 10 lines. Lines selected in the

high groups may have had a higher frequency of dominant favorable genes that could be designated the A' type, while the low groups may have had a high frequency of dominant, less favorable alleles of the A' type. Combinations such as A' A' on the average may exhibit little or no dominance in crosses between different populations. Cress (1966b) has shown algebraically that with multiple alleles some loci might make negative contributions to heterosis in crosses between populations, when the dominance relationships of all pairs of alleles are positive.

Since the two methods were positively correlated for selecting lines for high and low yield, some lines should be selected by both methods. In Population A, there were five lines common to both the HT and HS<sub>2</sub> groups and two lines common to both the LT and LS<sub>2</sub> groups. In Population B, there were two lines common to the high groups and one line common to the low groups. These results indicate that even though the two methods generally gave the same results, different lines were selected, because the above situation, except for the Population A high groups, could simply arise from chance alone.

Correlated responses of other traits to selection for high and low grain yield were apparently somewhat different for the two methods. Average ear weight differences between high and low selections were 16 grams for the Inbred Tester Method and only 2 grams for the S<sub>2</sub> Progeny Method. On the other hand, there was a larger difference between high and low groups for number of ears per plant with the S<sub>2</sub> Progeny Method (6.5 ears per 100 plants) than with the Inbred Tester Method (2 ears per 100 plants). Selection for high yield resulted in an average of 3 cm lower ear height than selection for low yield with the Inbred Tester Method, but there was no difference for this trait

with the  $S_2$  Progeny Method. Differences between methods for response of husk, ear quality, and root lodging scores and of percentage rotten ears and erect plants were very small.

Theoretically, the  $S_2$  Progeny Method should be more effective than methods involving a tester for changing frequencies of favorable genes, because dominant genes in the tester tend to mask expression of genes in the plant being tested. In  $S_2$  progenies at least 75% of the loci are homozygous, so there is a much lower probability of recessive alleles being masked by dominant alleles than with half-sib progenies. The results of this study show, however, that low yielding  $S_2$  lines are not necessarily low in combining ability with unrelated testers. This suggests that contributions of homozygous loci are in some way different from contributions of heterozygous loci, and that for combining ability improvement a tester should be used. This was a conclusion reached by Horner et al. (1973), who found that the Inbred Tester Method was more effective than the  $S_2$  Progeny Method for improving general combining ability.

The relatively high yields (Table 9) of the interpopulation crosses, AHT x BHT and AHS<sub>2</sub> x BHS<sub>2</sub>, indicate that the two populations combine well with each other. Additional cycles of selection by both methods should result in improved combining ability between the two populations and should provide some additional information on the relative efficiency of the methods.

## CONCLUSIONS

The  $S_2$  Progeny and the Inbred Tester Methods were equally effective in selecting lines for high combining ability, but the latter method was superior in selecting lines for low combining ability with unrelated doublecross testers. Evaluations based on synthetics and inter-population crosses indicated no significant difference between methods. These results show that lines selected by the Inbred Tester Method can be expected to combine well with unrelated populations. Therefore, this method should result in selecting lines for higher combining ability between the A and B populations.

The two doublecross testers were not as effective as the inbred testers for detecting small differences in combining ability among selected groups. The testcross data with the  $HS_2$  and the  $LS_2$  groups showed no significant difference when the doublecrosses were the testers. This shows that the inbred testers would be more effective than the heterozygous testers in improving frequency of genes having additive effects, because inbred testers can better discriminate between high and low combiners in the populations tested.

APPENDIX

Table 1  
 Mean Performance for Several Characteristics of Population A Lines Selected for  
 High and Low Yield by Two Methods when Crossed with Tester B.

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	%
Inbred Tester	kg/ha	g	cm	cm	score	score	%	score	score	%
High	5067a <sup>*</sup>	190	1.09	78	2.50	2.55	0.014	1.00	0.98	
Low	4188c	163	1.08	81	1.95	2.60	0.010	1.15	0.98	
Difference	879	27	0.01	-3	0.55	-0.05	0.004	-0.15	0.00	
S <sub>2</sub> Progeny										
High	4982ab	177	1.13	82	2.75	2.80	0.013	1.05	0.98	
Low	4637b	168	1.10	79	1.80	2.70	0.014	1.10	0.97	
Difference	345	9	0.03	3	0.95	0.10	-0.001	-0.05	0.01	

\*: Means in a column followed by different letters are significantly different at the 0.05 level.

Table 2  
 Mean Performance for Several Characteristics of Population A Lines Selected for  
 High and Low Yield by Two Methods when Crossed with Tester Coker 71.

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	
Inbred Tester	kg/ha	g	cm	cm	score	score	%	score	score	%
High	5306a*	179	1.26	86	2.35	2.95	0.012	1.65	0.96	
Low	4715c	163	1.22	90	2.95	2.90	0.033	1.95	0.96	
Difference	591	9	0.04	-4	-0.60	0.05	-0.021	-0.30	0.00	
S <sub>2</sub> Progeny										
High	4886ab	154	1.32	84	2.70	3.25	0.020	1.10	0.96	
Low	4564b	154	1.24	88	2.55	3.00	0.021	1.45	0.90	
Difference	322	000	0.08	-4	0.15	0.25	-0.001	-0.35	0.06	

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 3  
 Mean Performance for Several Characteristics of Population A Lines Selected for  
 High and Low Yield by Two Methods when Crossed with Tester Greenwood 471.

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	%
<u>Inbred Tester</u>	kg/ha	g		cm						%
High	5136a*	168	1.27	89	2.15	2.95	0.024	1.30	0.92	
Low	4703b	172	1.10	90	2.15	2.65	0.017	1.40	0.97	
Difference	433	-4	0.17	-1	0.00	0.30	0.007	-0.10	-0.05	
<u>S<sub>2</sub> Progeny</u>										
High	5301a	177	1.23	90	3.20	2.75	0.023	1.30	0.95	
Low	5124a	186	1.16	92	2.75	2.80	0.015	1.10	0.94	
Difference	177	-9	0.07	-2	0.45	-0.05	0.008	0.20	0.01	

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 4  
 Mean Performance for Several Characteristics of Population B Lines Selected for  
 High and Low Yield by Two Methods when Crossed with Tester A

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	
Inbred Tester	kg/ha	g		cm			%		%	
High	5312a*	172	1.34	75	2.90	2.95	0.009	1.00	0.97	
Low	4548b	150	1.31	82	3.50	3.00	0.014	1.15	0.90	
Difference	764	22	0.03	-7	-0.60	-0.05	-0.005	-0.15	0.07	
S <sub>2</sub> Progeny										
High	5038a	168	1.32	78	3.00	2.75	0.015	1.00	0.96	
Low	4540b	159	1.24	70	2.55	2.70	0.011	1.05	0.94	
Difference	499	9	0.08	8	0.45	0.05	0.004	-0.05	0.02	

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 5  
 Mean Performance for Several Characteristics of Population B Lines Selected for  
 High and Low Yield by Two Methods when Crossed with Tester Coker 71

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	%
<u>Inbred Tester</u>	kg/ha	g	cm	cm			%			%
High	5167a*	159	1.35	86	2.55	2.90	0.017	1.45	0.95	0.95
Low	4734b	150	1.27	86	3.25	2.95	0.005	1.70	0.95	0.95
Difference	433	9	0.08	00	-0.70	-0.05	0.012	-0.25	0.00	0.00
<u>S<sub>2</sub> Progeny</u>										
High	5176a	159	1.35	87	3.10	2.60	0.015	2.10	0.97	0.97
Low	5220a	159	1.34	88	2.15	2.80	0.015	1.75	0.96	0.96
Difference	-44	0	0.01	-1	0.95	-0.20	0.000	0.35	0.01	0.01

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 6  
 Mean Performance for Several Characteristics of Population B Lines Selected for  
 High and Low Yield by Two Methods when Crossed with Tester Greenwood 471

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	
	kg/ha	g		cm			%			%
<u>Inbred Tester</u>										
High	5041a*	168	1.26	86	2.15	3.00	0.014	1.20	0.96	
Low	4618b	150	1.28	90	2.60	3.10	0.010	1.15	0.92	
Difference	423	18	-0.02	-4	-0.45	-0.10	0.004	0.05	0.04	
<u>S<sub>2</sub> Progeny</u>										
High	5070a	172	1.20	92	2.35	2.70	0.011	1.10	0.95	
Low	5020a	168	1.20	88	2.05	2.70	0.005	1.40	0.97	
Difference	50	4	0.00	4	0.30	0.00	0.006	-0.30	-0.02	

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 7  
 Mean Performance for Several Characteristics of Population A Synthetics for  
 Two Methods of Selection

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	%
	kg/ha	g	cm	cm	score	score	score	score	score	%
<u>Inbred Tester</u>										
High	4963a*	159	84	3.87	2.43	0.007	1.07	0.92		
Low	4458b	141	86	2.51	2.27	0.021	1.03	0.96		
Difference	505	18	-2	1.30	0.16	-0.014	0.04	-0.04		
<u>S<sub>2</sub> Progeny</u>										
High	5003a	163	83	2.90	2.67	0.010	1.10	0.92		
Low	4240b	150	84	2.97	2.37	0.018	1.17	0.93		
Difference	763	13	-1	-0.07	0.30	-0.008	-0.07	-0.01		

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 8  
 Mean Performance for Several Characteristics of Population B Synthetics for  
 Two Methods of Selection

Methods of selection	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	
Inbred Tester	kg/ha	g	cm	cm			%			%
High	5477a*	181	1.26	87	2.50	2.17	0.006	1.03	0.96	
Low	4891b	159	1.25	91	4.13	2.83	0.013	1.01	0.89	
Difference	586	22	0.01	-4	-1.63	-0.66	-0.007	0.02	0.07	
S <sub>2</sub> Progeny										
High	5360a	159	1.35	91	2.33	2.30	0.003	1.03	0.95	
Low	4717b	172	1.19	92	2.30	2.10	0.007	1.17	0.92	
Difference	643	-13	0.16	-1	0.03	0.20	-0.004	-0.14	0.03	

\* Means in a column followed by different letters are significantly different at the 0.05 level.

Table 9  
 Mean Performance for Several Characteristics of Interpopulation Crosses.

Crosses	Characteristics									
	Grain yield	Ear weight	Ears per plant	Ear height	Husk score	Ear quality score	Ears rotten	Root lodging score	Plants erect	
	kg/ha	g	cm	cm			%		%	
AHT x BHT	5383a*	178	1.29	89	3.10	2.75	0.009	1.15	0.92	
ALT x BLT	4689d	154	1.25	93	3.35	2.60	0.009	1.60	0.89	
Difference	694	24	0.04	-4	-0.25	0.15	0.000	-0.45	0.03	
AHS <sub>2</sub> x BHS <sub>2</sub>	5529a	168	1.36	91	3.10	2.55	0.011	1.55	0.93	
ALS <sub>2</sub> x BHS <sub>2</sub>	4937bcd	168	1.21	94	2.70	2.40	0.006	1.30	0.89	
Difference	592	0	0.15	-3	0.40	0.15	0.005	0.25	0.04	
AHT x BLT	5281ab	163	1.31	91	4.00	3.05	0.003	1.40	0.92	
ALT x BHT	4837cd	172	1.17	94	2.35	2.20	0.012	1.40	0.95	
Mean	5059	167	1.24	92.5	3.17	2.62	0.007	1.40	0.93	
AHS <sub>2</sub> x BLS <sub>2</sub>	5111abc	163	1.31	88	3.50	2.65	0.020	1.25	0.90	
ALS <sub>2</sub> x BHS <sub>2</sub>	4948bcd	177	1.17	92	2.70	2.40	0.006	1.30	0.91	
Mean	5029	170	1.24	90	3.10	2.52	0.013	1.27	0.905	

\*: Means in a column followed by different letters are significantly different at the 0.05 level.

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## BIOGRAPHICAL SKETCH

Mesfin Ameha was born on April 30, 1942 in Huruta, Arusi, Ethiopia. He graduated from Jimma Agricultural and Technical High School, Ethiopia, in 1965. The same year, he enrolled at Haile Selassie First University, now called Addis Ababa University, the College of Agriculture, Alemaya. After completing the third year study, he participated in the Ethiopian University Service program working for the Swedish Mission in Backo, Shoa, as a school teacher and farm manager for one year. The following year, in July, 1970, he received the Bachelor of Science Degree in Agriculture.

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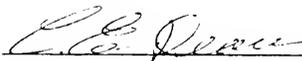
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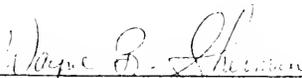
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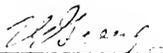
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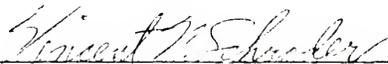
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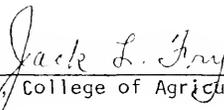
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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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