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# Relation among full-sib progenies of maize (Zea mays L.) for different generations of inbreeding

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Iowa State University, 1988



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Relation among full-sib progenies of maize (Zea mays L.) for different generations of inbreeding

of

Omar Alexis Rodriguez

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department: Agronomy Major: Plant Breeding and Cytogenetics

# Approved:

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# TABLE OF CONTENTS

	Page
INTRODUCTION	1
LITERATURE REVIEW	4
Recurrent Selection	4
Reciprocal Full-sib Selection	5
Response to Recurrent Selection	7
Early Generation Testing	9
Genetic Variation	14
Genetic Correlations	18
MATERIALS AND METHODS	22
Field Procedures	24
Statistical Procedures	27
RESULTS AND DISCUSSION	36
SUMMARY AND CONCLUSIONS	95
LITERATURE CITED	99
ACKNOWLEDGMENTS	105

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#### INTRODUCTION

An increase in production of food is needed in the future to satisfy the basic nutritional requirements of an expanding world population. Plant breeders need to be more efficient in the creation of better and more productive cultivars. Hence, any improvement of the available breeding techniques is going to help meet these goals.

In its broadest sense, recurrent selection can be defined as any breeding system that includes crossing of selected individuals, followed by further selection and recombination of selected individuals. Recurrent selection methods were developed to exploit the phenomenon of heterosis (interpopulation improvement) and to emphasize the additive effects of genes (intrapopulation improvement). The primary objective of plant breeding programs is to identify superior genotypes or combinations of genotypes (Hallauer, 1986).

Hallauer (1973) emphasized that there are two distinct phases of maize (Zea mays L.) breeding necessary for systematic improvement: (1) development and improvement by recurrent selection of the breeding populations, and (2) the efficient extraction of lines and identification of hybrids. Hallauer and Eberhart (1970) proposed a breeding method, reciprocal full-sib selection, where nonadditive genetic effects, as well as the additive effects, are included in selection. Gardner (1978) suggested that full-sib reciprocal recurrent selection seems exceptionally promising from a commercial maize breeding standpoint, because new hybrids become available each cycle while the populations and their interpopulation crosses are being improved.

Genetic variability is essential for effective selection. Hence, the relative amount of genetic variability within and among populations is important to determine the relative progress that can be expected from selection. The genetic portion of the variance of tested progenies from full-sib families is greater than half-sib families. Use of  $S_1$ progenies as parent of full-sib families to increase the variance among full-sib families by the factor of (1 + F) was suggested by Sprague and Eberhart (1977).

The correlation coefficients may be considered as a measure of the commonness of the genes governing the determination of two traits and the relationship between parent and offspring. Hence, the correlation data between traits of parent plant and its progeny may be used to assist in the selection of progenies. Correlations between traits indicate expected correlated responses that occur with selection, whereas correlations between parent and offspring indicate expected effectiveness of selection.

Reciprocal full-sib selection has been a productive breeding technique. It is extremely efficient in that the yield trials for population improvement also serve as early testing for inbred selection and hybrids combinations. Reciprocal full-sib selection was initiated by Hallauer (1967a) to improve two populations and to develop hybrids.

Reciprocal full-sib selection is based on early testing, in its truest sense. There are differences of opinion on the value of early testing; thus, it is important to determine the relationship among generations of testing on successive generations of inbreeding.

The objectives of this study were: (1) to estimate the variability

among full-sib crosses for five generations of inbreeding to determine changes in variability among full-sib progenies with generations of inbreeding; and (2) to estimate the genotypic correlations between fullsib progenies of different generations of inbreeding to determine if a trend occurs with increased generations of inbreeding of lines used to produce full-sib progenies.

#### LITERATURE REVIEW

#### **Recurrent Selection**

Recurrent selection is a common method of population improvement where a selected group of genotypes from a heterogenous population are ultimately intercrossed to provide a new segregating population for another cycle of selection. Thus, recurrent selection is a cyclic process of selection and intermating of selected genotypes. These procedures maintain genetic variability and permit the increase of the frequency of desirable alleles and gene combinations by recombination of selected genotypes. Recurrent selection schemes were proposed to remove some of the restrictions encountered in the early classical breeding methods (Hallauer and Miranda, 1981).

The general method was outlined by Jenkins (1940). In 1945, Hull introduced the term "recurrent selection" to emphasize the importance of frequent recombinations in an efficient breeding system. Hallauer (1980a) described recurrent selection as a breeding method that included three phases: (1) development of progenies: (2) evaluation of progenies in replicated trials, and (3) recombination of superior progenies to form the next cycle population for continued selection. Because mass selection is based on selection among individuals, plants that are not replicated, it is the exception to the three-phase scheme. Several methods of recurrent selection suggested for use in the improvement of crop species were given by Sprague and Eberhart (1977), Hallauer and Miranda (1981), and Hallauer (1981a, 1986). The differences among methods

are based on the basic unit used for selection, the population size, objectives, and traits under selection.

Hallauer and Miranda (1981) pointed out that the development and use of different methods of recurrent selection have emphasized early testing for discriminating among progenies to determine which ones to recombine to form the next cycle of selection. Further, they emphasized that the objective of early testing in recurrent selection is the same as originally proposed for early testing: to identify genotypes that have good and poor combining ability (Sprague, 1946). They presented experimental evidence that indicates that long-term cyclical selection programs have been effective for improvement of yield and other important agronomic traits.

#### Reciprocal Full-sib Selection

Recurrent selection methods were designed to gradually increase the frequency of favorable alleles for the trait under selection. The ultimate use of the products of recurrent selection is to provide improved germplasm sources for applied breeding programs. Various schemes have been proposed to improve heterogeneous populations as source material for the production of new improved hybrids. Hallauer and Eberhart (1970) suggested reciprocal full-sib selection as a procedure designed to maximize selection for nonadditive genetic effects as well as additive genetic effects. Hallauer (1967a, 1967b) and Lonnquist and Williams (1967) described the techniques used to produce the hybrid and selfed seed on the same plants. The breeding system proposed by Hallauer and Eberhart (1970) has two separate aspects that are conducted

simultaneously: (1) evaluation of the  $S_0$  by  $S_0$  plant crosses (full-sib progenies for population improvement) and (2) early testing of potential single-cross combinations ( $S_0 \times S_0$  plant crosses). Furthermore, selfed seed of the parents of superior yielding  $S_0$  by  $S_0$  crosses is also used for recombining to form the two improved populations for continued selection, as reported by Comstock et al. (1949) for reciprocal recurrent selection. Reciprocal full-sib selection has the advantage that selfed seed of the parents of superior  $S_0$  by  $S_0$  crosses can be planted ear-to-row for continued selfing and crossing for the rapid development of new single crosses (Hallauer, 1967a; 1967b). Eberhart and Russell (1969) emphasized that the procedure proposed by Hallauer (1967a) and Lonnquist and Williams (1967) for selection of superior single crosses seems to have merit for the production of superior and stable single crosses. The advantage is that the full-sib progenies have greater variation than half-sib progenies because full-sib progenies include both additive and nonadditive effects. If nonadditive effects are important, reciprocal full-sib selection includes them in selection, whereas reciprocal half-sib recurrent selection includes only additive effects.

Systematic genetic advance in maize hybrids depends on the successive improvement of breeding populations and on the efficiency of the extraction of inbred lines. Reciprocal full-sib recurrent selection was designed to improve two breeding populations and to extract superior inbred lines (Hallauer and Eberhart, 1970). It is extremely efficient in that the yields trials for population improvement also serve as early testing for inbred selection and hybrids. Suwantaradon and Eberhart

(1974) reported that an efficient development of hybrids from varieties under population improvement includes three phases: (1) early testing provided by selection trials for the next cycle of recurrent selection; (2) preliminary evaluation of hybrids using early-generation lines to identify superior hybrids; and (3) final evaluation of advanced-generation lines in superior hybrid combinations as identified in phase 2. Reciprocal full-sib selection was used by Hallauer (1973) to improve two populations and to develop hybrids simultaneously.

#### Response to Recurrent Selection

Recurrent selection has been shown to be effective in the improvement of agronomic traits in maize. The effectiveness of reciprocal recurrent selection was estimated (Moll and Robinson, 1966; Martin and Hallauer, 1980) and compared with other methods of selection (Moll and Stuber, 1971; Eberhart et al., 1973; Moll et al., 1978; Smith, 1983). Penny et al. (1967) concluded that recurrent selection seems to be a useful breeding procedure for improvement of varieties for resistance to insects and diseases. Sprague and Brimhall (1950) and Sprague et al. (1952) reported that recurrent selection was effective to increase oil content of maize. Moll and Stuber (1971) concluded that full-sib selection and reciprocal recurrent selection have resulted in increased yield of the hybrids without adverse effects upon agronomic acceptability in terms of plant height, ear height, and flowering. Rodriguez and Hallauer (1988) compared the relative effectiveness of different methods of recurrent selection in maize populations and reported that a positive response to selection for yield was accomplished without selection for

taller, later maturity genotypes. Further, tassel branch number decreased significantly with selection for greater grain yield in all instances. No consistent trends were detected for changes in root and stalk lodging with selection for grain yield. Sprague and Brimhall (1950) were the first to report the effectiveness of recurrent selection for specific combining ability.

Reciprocal full-sib selection was effective in developing highyielding hybrid combinations (Hallauer, 1973; Hoegemeyer and Hallauer, 1976; Hallauer, 1984a). Jones et al. (1971) compared algebraically and with computer simulation reciprocal full-sib recurrent selection and halfsib reciprocal recurrent selection. They showed that reciprocal full-sib recurrent selection, as suggested by Hallauer and Eberhart (1970), was a more efficient method of selection in some instances than reciprocal recurrent selection suggested by Comstock et al. (1949). Further, they emphasized that reciprocal full-sib selection enables breeders to combine the efficient development of new hybrids with population improvement, and it should prove a valuable technique in plant breeding. Obilana et al. (1979) reported experimental evidence confirming the effectiveness of the reciprocal full-sib selection method in improving maize populations and their crosses. Lamkey and Hallauer (1987) reported that on a per-year basis, full-sib reciprocal recurrent selection had the greatest interpopulation improvement.

Detailed summaries of results from studies on recurrent selection were given by Sprague and Eberhart (1977), Hallauer and Miranda (1981), and by Hallauer (1986). In most instances, rates of response to

selection for yield improvement were similar (2 to 4% per cycle) for the different methods of recurrent selection (Hallauer and Miranda, 1981).

#### Early Generation Testing

Modern commercial production of maize is based on maize hybrids, involving four, three, or two parental inbred lines. The development of inbred lines poses no problems equal in complexity to the problems involved in the evaluation of lines. The final evaluation of the most carefully selected inbred lines must depend upon its performance in hybrid combinations. Therefore, one cannot put together any two inbred lines at random and expect them to result in a satisfactory single-cross hybrid. Adequate selection and testing are necessary to isolate desirable cross combinations, and this effort is greater when three-way and double-cross combinations are considered.

Therefore, it is immediately apparent that the maize breeder needs to solve two major problems. The first of these concerns the time at which testing of inbred lines should begin and the second is the problem of what to use as a tester. Among maize breeders there are two schools of thought regarding the stage in the development of an inbred at which testing should begin. One group advocates early testing in which  $S_0$ plants are outcrossed to a tester at the time of first selfing. Performance of the test crosses is then used as a guide to determine whether or not further selfing of the  $S_0$  plant is justified. Proponents of the early testing idea feel that a higher percentage of undesirable lines of a population can be discarded following the first test before further time and expense are expended in inbreeding and testing.

The early generation testing procedure was first suggested by Jenkins (1935), who reported that early testing of maize lines would be effective after the second generation of inbreeding. He found that inbred lines of maize showed their individuality as parents very early in the inbreeding process and remained relatively stable thereafter. For that reason, it was suggested that from the standpoint of practical maize breeding, it is important to know the earliest possible generation in which newly developed lines may be tested for yield performance. Early elimination of unpromising lines permits a concentration of effort on more promising material and should result in greater progress in the breeding operations (Jenkins, 1940).

Those who oppose early testing believe that the performance of an  $S_0$  plant is not indicative of its performance in later generations. Further, they emphasize that visual selection is effective in improving combining ability during the early inbreeding generations and that many worthwhile lines may be discarded on basis of topcross test in the early generations. Richey (1945) reanalyzed Jenkin's 1935 data, and concluded that elimination on the basis of topcross tests in the  $S_1$  generation would have resulted in the loss of several lines which ultimately (in  $S_8$ ) were as high in combining ability as those obtained from the better  $S_1$  families. Lonnquist (1950) pointed out that Richey's analysis was based on a method of grouping lines which showed similar divergent trends as inbreeding progressed. These trends were not subject to statistical analysis and could not be so treated, as pointed out by Jenkins (1935). Richey (1945) emphasized, based on his analysis, that the use of either

selfed or crossed progeny performance as a basis for selection among or within families in the initial stages of breeding program was not warranted.

Early testing is a procedure designed to evaluate genotypes during early stages of inbreeding. It is different from the usual inbreeding and testing procedures because  $S_0$  plants are outcrossed to a tester at the time of the first selfing and are culled before time and money are invested in inbreeding and testing these lines. Therefore, early generation testing is practiced for inbred lines in which full homozygosis has not been attained to eliminate the undesirable genotypes from further testing and inbreeding.

The procedure that permits the greatest gain per unit of resource input should be used by the breeder to increase his efficiency. Lonnquist (1950) suggested that the earlier the lines can be evaluated for combining ability, the more efficient the selection program will become. Further, he reasoned that if such tests can be made early in the inbreeding program, more intensive selection can be made for other important agronomic traits. It is clear that maximum efficiency and progress in breeding for any trait can be obtained if the best genotypes can be selected in the earliest generation so that they will be retained for further testing.

Mayo (1980) stated that one reason why some breeders have strongly advocated early generation selection for yield is because in any particular cross, plants containing many favorable genes (in

heterozygous state) will be far more common in the  $S_0$  and  $S_1$  than in later generations.

Sprague (1946) reported that the value of early testing will be materially affected by the general level of desirability of the parental material available. Genter (1963) emphasized that the accurate identification and evaluation of superior germplasm were probably the most important task that faces maize breeders. Without this positive identification, selection of elite inbred lines becomes a matter of chance.

Hallauer and Miranda (1981) emphasized that the potential ceiling of any derived line is determined at the time of the first selfing generation of an  $S_0$  plant. Further, they suggested that better sampling techniques may be used if material could be discarded in early generations of inbreeding. Thus, they insisted that greater attention and effort could be expanded on selection within progenies of genotypes saved on the basis of the preliminary early yield-test information.

Recurrent selection is based primarily on early testing results. Evaluation during early segregating generations permits rapid elimination of inferior segregates and, thereby, enhances the probabilities of obtaining desirable combinations by increasing the frequency of desirable alleles in the remaining population. Hallauer and Miranda (1981) and Hallauer (1981a, 1986) presented experimental evidence of the success that has been achieved by recurrent selection.

Genotypes cannot transmit genes that they do not carry. Therefore, it is expected that the lines that combine well with other lines must possess either a larger number of superior genes or major genes for the

agronomic traits that contribute to vigorous plant development and high yield. The most productive inbred lines tend to make the highest yielding crosses, and the poorest inbreds tend to make the poorest crosses. On the average, productive homozygous inbred lines will more likely be developed from productive S1 progenies. Lonnquist (1950) reported that  $S_1$  lines, with high combining ability, resulted in  $S_4$  lines with high combining ability, and that S<sub>1</sub> lines with low combining ability resulted in  $S_{L}$  lines with low combining ability. Genter and Alexander (1966) reported in recurrent selection study, that the more productive S, lines tended to make the more productive crosses. Further, they reported that discarding in each generation tended to be most severe among those progenies derived from lower yielding S1 lines. Hallauer and Lopez-Perez (1979) reported that the higher yielding  $S_g$  testcrosses generally came from the same lines that had higher yielding  $S_1$  testcrosses. Suwantaradon and Eberhart (1974) emphasized that the preliminary evaluation of hybrids using early-generation lines should be used to identify superior hybrid combinations. Furthermore, selection among  $S_3$  or  $S_4$  sublines from elite S<sub>1</sub> lines could give additional improvement. After superior yielding hybrid combinations have been identified, selection for other agronomic traits should be practiced among sublines in the inbreeding program before the advance-generation lines are evaluated as single-cross hybrids in the final evaluation.

Hallauer and Miranda (1981) indicated that some form of early testing is used in most maize breeding programs regardless of the intention of the plant breeder. Experience suggests that, in general,

those lines with the best general combining ability also tend to make the best specific crosses, and that the inbreds that make occasional superior crosses are much less desirable.

## Genetic Variation

Phenotypic diversity within natural populations is impressive even with the most casual observation. Hence, plant breeders planning a breeding program must consider this phenotypic diversity and determine the proportion and nature of the phenotypic diversity that is attributable to genetic causes. To discern the mode of inheritance of a trait under study, the plant breeder must differentiate the genetic from nongenetic components of variation.

Genetic advance through selection is the primary objective of plant breeding. Effective selection of genetically superior individuals depends on the existence of adequate genetic variation in the original population and the heritability must be sufficiently high for effective selection.

Genetic variability arises from the contribution of segregating genes and their interaction with other genes. Variation is classified as qualitative when genotypes can be assigned to a few discrete classes and as quantitative when genotypes exhibit a continuous distribution. The breeder is mainly concerned with those traits that express continuous variation. These traits are designated quantitative traits because they are inherited in a multifactorial fashion and are influenced by the environmental effects. Knowing the genetic characteristics information of breeding populations is important in designing effective breeding

systems. The relative amount and types of genetic effects that contribute to the quantitative variation of traits are important in planning breeding strategies.

Genetic variance of quantitative traits includes the variance among breeding values, called additive genetic variance  $(\sigma_A^2)$ , the variation due to dominance deviations, called dominance genetic variance  $(\sigma_D^2)$ , and the interaction among loci, or epistatic variance  $(\sigma_I^2)$  (Falconer, 1981). The additive genetic variance is the most important because it is the primary cause of resemblance between relatives and is the main determinant of the response of populations to selection. Hallauer and Miranda (1981) summarized experimental results of maize populations, and the additive genetic variance was the most important contributor to total genetic variance. Variance due to dominance effects was of less importance, and epistatic variance seemed to be of minor importance. The environmental conditions under which the populations were grown may influence the relative magnitude of the genetic and nongenetic causes of variation of quantitative traits.

Genetic variability is essential for effective selection, but Hallauer (1980a) emphasized that availability of genetic variability is not the only factor. To ensure future genetic progress, it is important also to upgrade the general level of performance of populations. Further, he stated that there are two forces that seem antagonistic: (1) improving the populations by increasing the frequency of favorable alleles, which reduces genetic variability (depending on gene frequency when selection started); and (2) maintaining genetic variability for

future selection. Therefore, the breeder is restricted to maintaining the variability of his crop species, by using recurrent selection, which are long-term breeding methods that maintain and include regeneration of variability by recombination of selected genotypes (Hallauer, 1980a). Sprague (1946) emphasized that the efficiency of continued detailed testing, as inbreeding progresses, depends on the relative variability in  $S_0$  vs  $S_1$ ,  $S_1$  vs  $S_2$ , etc. Sprague (1946) also stated that genetic variability decreased by approximately one-half within progenies with each additional generation of self-pollination. Therefore, any decision as to the efficiency of testing topcrosses in successively later generations must be influenced by the amount of variability present in the preceeding generation and the indicated superiority of the line in question.

The relative amount of genetic variability within and among populations is important to determine the relative progress that can be expected from selection. For example, the genetic portion, assuming only additive and dominant effects, of the variance among full-sib families  $(1/2\sigma_A^2 + 1/4\sigma_D^2)$  is greater than half-sib families  $(1/4\sigma_A^2)$ . Inbreeding will increase the variance among families by the factor of (1 + F), where F is the coefficient of inbreeding of the parents. The coefficient of the  $\sigma_D^2$  changes also. Cockerham (1963) showed that the genetic variances among relatives increases with inbreeding.

To predict the relative response to selection, it is necessary to determine the magnitude and type of genetic variation present in the

breeding population. Thus, these estimates can be used to predict progress from selection and to help in determining the most appropriate breeding scheme. To obtain estimates of the relative magnitude of the genetic parameters in maize, several methods and genetic materials have been used; many of them were reported by Hallauer and Miranda (1981). Cockerham (1963) reported that the estimates of genetic, environmental, and genetic-environmental interaction components of variance can be obtained from the appropriate analysis of variance for the mating designs used in developing progenies. Eberhart et al. (1966) emphasized that reliable estimates of genetic variances with small standard errors can only be obtained from large experiments, repeated over an adequate sampling of environments. Wright et al. (1971) reported that regardless of the estimation procedure used, the largest proportion of the total genetic variance was additive for all traits, and in general, these results agree with those obtained by using simpler mating designs for maize populations. Obilana and Hallauer (1977) concluded that valid estimates of genetic variability can be obtained in less time and at a cheaper cost from noninbred materials. Further, they emphasized that estimates from the selection experiments also can be used to predict genetic advance, which can be compared with the empirical results to determine the relative efficiency of selection. Obilana et al. (1979) studied three procedures to obtain estimates of genetic, environmental, and genetic x environmental variances for nine traits. The target population was the interpopulation formed by crossing the two popula-

tions. They reported that the estimates obtained from the interpopulation were similar to those reported for intrapopulations of maize.

## Genetic Correlations

In maize breeding programs, several systems have been used in inbred development and evaluation. One system is based on visual selection among and within ear-to-row progenies for several inbreeding generations before evaluation for hybrid performance (Russell, 1985). Because selection is based mainly on visual traits, it is necessary to determine the relationship between such traits and the performance of the line and its hybrid progeny.

Plant breeders have always been concerned with the extent to which desired traits are transmitted from superior plants to their progenies. Correlation coefficients have been used to express the level of this relationship. The level of association between two traits, both genetic and nongenetic, is usually measured by the correlation coefficient. Studies examining the relationships between traits within and between generations have been reported. Jenkins (1929) reported that after only 3 or 4 generations of inbreeding, lines must be homozygous for many factors that affect yield. Genter and Alexander (1966) suggested that the correlation between yields of inbred lines and their crosses seems to be affected by the level of homozygosity of the lines. Johnson et al. (1955) emphasized that environmental effects accounted for the failure of the yields of lines to be indicative of the yields of their progenies. Whan et al. (1981) concluded that the level of homozygosity of a trait in a particular generation is an important factor that determines the

correlation between generations and the predictive value of the material.

In order to use the progeny yield data to determine which progenies shall be retained and which shall be discarded, the correlation data between traits of the parent plant and its progeny may be used. In general, it is assumed that the parents must contain those factors which determine whether the progenies have high, average, or low productivity. Coefficients of correlation, therefore, provide a measure of the commonness of the genes governing the expression of two traits. If two traits have no genes in common, they are expected to be uncorrelated. When measurable traits are correlated, it is because they share at least a proportion of the genes that are involved in their expression.

The breeding procedure designated by Hallauer (1967a) and Lonnquist and Williams (1967) for obtaining single-cross hybrids from full-sib families was examined theoretically by Miranda-Filho and Hallauer (1978). They investigated the relationship between progenies in different generations by use of correlations and regressions. Their study was done considering only one population which was characterized by variation in gene frequencies as intermediate (P = 1/2), low (P = 1/3), and high (P = 2/3). They concluded the genetic correlations showed that selection among S<sub>0</sub> plants assures the best performance of S<sub>1</sub> progenies but not necessarily the best performing S<sub>0</sub> x S<sub>0</sub> and S<sub>1</sub> x S<sub>1</sub> full-sib families. In a more recent paper, Miranda-Filho et al. (1982) investigated theoretically the genetic potential of the breeding procedure designed to obtain singlecross hybrids from full-sib progenies when two base populations are used in crosses. They investigated the theoretical relations between popula-

tion means in the method of hybrid development from interpopulation full-sib progenies. The focus was on the intrinsic genetic properties of the method and was based on approximate expected values of correlation and regression coefficients by varying gene action and population structure. They concluded that selection among  $S_0 \times S_0$  full-sib progenies based on replicated trials is potentially very effective for identifying superior  $S_1 \times S_1$  crosses. The general results for two populations did not differ greatly from those reported for a single population (Miranda-Filho and Hallauer, 1978), although numerical values of correlation and regression coefficients were generally lower. Again, the level of dominance effects had a greater effect on the correlation and regression coefficients than did the structure of the populations.

Genetic correlations also are of interest because they can affect the amount of change which can be brought about in one trait by artificial or natural selection for the other trait. The genotypic correlation between two traits also is expected to be a better criterion of their relationship than the phenotypic correlation. The parentprogeny correlations are more important as guides for selection because they measure the general tendency toward resemblance in the traits under study. The level of resemblance may be expressed by regression or correlation coefficients. Cockerham (1961) reported that the covariation observed between any two relatives may be interpreted in statistical genetic terms as genotypic covariances among relatives, and, accordingly, each genetic covariance may be given a series of coefficients of correlation to indicate its level of genetic relationship. Estimates of

genetic covariances can be used to predict correlated responses to selection and to rank prospective parents on the base of multivariate data.

Falconer (1952) extended the idea of genetic correlation to include the interaction of the same trait of the same genetic groups to two different environments. Further, he suggested that a trait measured in two different environments should be considered not as one but as two traits associated by a genetic correlation. Yamada (1962) concluded that if it is assumed a trait under two different environments is not the same, the relationship of the trait under different environments should be expressed in terms of genetic and environmental correlations. Yamada's (1962) conclusion was made because genes which control the trait under a particular environment may be either different or partially different from those genes which control the trait under a different environment.

#### MATERIALS AND METHODS

The plant materials used in this study were derived from the two 2-eared maize populations, 'Pioneer Two-ear Composite' (BS11) and 'Iowa Two-ear Synthetic' (BS10). BS11 was developed by W. L. Brown of Pioneer Hi-Bred International Inc. by crossing southern prolific materials with Corn Belt inbred lines. BS10 was developed by W. A. Russell of the Iowa Agriculture and Home Economics Experiment Station by recombining 10 inbred lines that expressed a prolific tendency in the maize breeding nursery (Hallauer, 1967a).

Each cycle of selection was completed in two years with each cycle requiring three seasons: full-sib crosses of  $S_0$  plants and selfs of  $S_0$  plants were made at Ames (Iowa) in the summer (season 1); full-sib crosses were evaluated in replicated trials in Iowa in the summer (season 2); and recombination of  $S_1$  progenies of superior full-sib crosses was completed in Puerto Rico winter nursery (season 3). The trait of primary interest was yield. Other agronomic traits also were considered in selection (Hallauer, 1984b).

Two sets of  $S_1$  progenies, one set for each of two populations, were used to produce cycle five (C5) of reciprocal full-sib recurrent selection in BS10 and BS11. Twenty  $S_1$  progenies for each population were planted in the 1977-78 Puerto Rico winter nursery. The partial diallel method of recombination was used to intermate the 20 selections. Two replications of recombinations for each population were included to ensure that a representative sample of genes for each selection was included in each population. Harvested ears were counted and equal

quantity of seeds was taken from each ear to form a composite (Hallauer, 1977). In the C5 cycle of reciprocal full-sib selection in BS10 and BS11, full-sib progenies for the first five generation of inbreeding  $(S_0, S_1, S_2, S_3, \text{ and } S_4)$  were evaluated.

Hallauer (1984b) presented details of how the materials for this study were produced. Selections were based on  $S_0 \propto S_0$  crosses to form the next cycle population; remnant  $S_1$  seed of 20 selections were recombined in the Puerto Rico nurseries. The initial crosses for the C5 cycle were produced in 1978 for testing in 1979. Over 300  $S_0 \times S_0$  crosses were successful in 1978, but selection after infestation for European corn borer (Ostrinia nubilalis) resistance and after inoculation with a spore suspension of Diplodia zeae for stalk rot resistance reduced the number of crosses for testing to 156. From the crosses and selfs produced in 1978, 156 full-sib progenies were tested in replicated trials conducted at three locations in 1979. The 156 pairs of S<sub>1</sub> progenies also were planted in the breeding nursery to produce  $S_1 \propto S_1$  crosses and  $S_2$  progenies of the parents used in the crosses. This method was repeated in each generation of inbreeding until  $S_4$  generation. Therefore, data relative to full-sib progeny performance were available in successive generations of inbreeding. After the  $S_{\underline{\lambda}}$  generation, the lines were continued in the breeding nursery for further inbreeding. The  $S_7$  generation seed was produced in 1984 for most lines, but some were completed in 1985 because of poor stand or damage from heat and drought stress at flowering time in 1984. The schedule of activities for the C5 generations selfs and full-sib progenies is as follows:

		Activity			
Year	Inbreeding (F)	Nursery	Performance trials		
	%				
1978	0	C5 - S <sub>0</sub> x S <sub>0</sub> crosses	4) iii ai ii		
1979	50.00	C5 - S <sub>1</sub> x S <sub>1</sub> crosses	S <sub>0</sub> x S <sub>0</sub> crosses tested		
1980	75.00	$C5 - S_2 \times S_2$ crosses	S <sub>1</sub> x S <sub>1</sub> crosses tested		
1981	87.50	C5 - S <sub>3</sub> x S <sub>3</sub> crosses	S <sub>2</sub> x S <sub>2</sub> crosses tested		
1982	93.75	$C5 - S_4 \times S_4$ crosses	$S_3 \times S_3$ crosses tested		
1983	96.88	S <sub>5</sub> lines selfed	$S_4 \times S_4$ crosses tested		
1984	98.44	S <sub>6</sub> lines selfed	$S_4 \times S_4$ crosses tested		
1985	98.44	S <sub>6</sub> lines selfed			
1986	99.22	S <sub>7</sub> lines selfed			

There were 156  $S_0 \times S_0$  crosses produced in 1978 for testing in 1979. Every attempt was made to continue each line, but some were lost because of nicking at flowering time, poor seed set, and diseased seed. It was not possible to continue 20 pair of lines as homozygosity increased. No selection was practiced among the full-sib progenies for the different generations of inbreeding. Therefore, 136 crosses were successful in each of the generations of inbreeding and testing for this particular study. To achieve the perfect number of 169 entries for each generation, some other entries must be added.

# Field Procedures

Three experiments were conducted for each generation in each year except for the  $S_4 \times S_4$  generation crosses which included data for one experiment in 1983 and two for 1984 (Hallauer, 1984b). All experiments were machine planted and harvested and included two replications at each location. Data were collected in all experiments for stand (plants ha<sup>-1</sup>), root lodging (plants leaning more than 30° from vertical), stalk lodging (plants broken at ear node or below), dropped ears (%), yield (q ha<sup>-1</sup> at 15.5% grain moisture), and grain moisture (%).

The experimental design was a 13 x 13 simple lattice at each location. Two-row plots that were 5.3 m long with 75 cm between rows were used at each location. Planting density was 52 plants/plot or 65,408 plants/ha. Conventional culture practices of fertilization and weed control were used at all locations to promote high productivity.

In addition to the full-sib progenies, 13 check entries were included in all trials to provide a base for comparison of full-sib progenies in succeeding generations of inbreeding. The check entries included in this study are shown in Table 1.

	Year of testing						
Entry	1979	1980	1981	1982	1983	1984	
BS10C0	+ <sup>a</sup>	+	+		+	+	
BS11C0	+	+	+	+	+	+	
BS10C5	+	+	+	BS10C6	+	+	
BS11C5	+	+	+	BS11C6	+	+	
BS10C0 x BS11C0	+	+	+	+	+	+	
BS10C5 x BS11C5	+	+	+	<b>BS10C6 x BS11C6</b>	+	+	
B37 x Oh43	+	+	+	+ .	+	+	
B45 x CI31A	+	+	+	+	+	+	
B14A x B45	+	+	+	+	+	+	
AES704	+	+	+	+	+	+	
IA5115	+	+	+	+	+	+	
IA516	+	+	+	+	+	+	
Farmer entry	+	+	+	+	+	+ .	

Table 1. List of check entries included in each of the evaluation trials of full-sib progenies for each generation of inbreeding

a+ the same as the year before.

Estimates of variance and genotypic correlations were of special importance in these studies. To provide an estimate of experimental error, the full-sib progenies were replicated in the different yield trials. Random allocation of genotypes to plots in each replication of each experiment was conducted to provide an unbiased estimate of error. Therefore, it was expected that every plot had the same probability of receiving a specified genotype and systematic variation due to soil heterogeneity is transformed to independent and random variation in relation to genotypes. Different locations were considered to give unbiased estimates of genetic variance. The use of environments provided an estimate of genetic variance and genotype by environment variance for each generation of testing. The locations used for the evaluation of the full-sib progenies are listed in Table 2.

Fyneriment	Year of testing					
number	1979	1980	1981	1982	1983	1984
25	Ames <sup>a</sup>	Ames	Ames	Ames	Ames	
26	Ankeny	Ankeny	Ankeny	Columbia		Ames
27	Martins- burg	Martins- burg	Martins- burg	Martins- burg		Columbia

Table 2. Experiment numbers and locations used for the evaluation offull-sib progenies for each generation of inbreeding

<sup>a</sup>Ames, Ankeny, and Martinsburg, Iowa, and Columbia, Missouri, respectively.

#### Statistical Procedures

Analyses of variance were conducted for each experiment in one location and combined over locations for the same year. A combined analysis of variance was computed for the 1983 experiment and the two 1984 experiments. Field design was a 13 x 13 simple lattice with two replications conducted at each location. Years and locations were considered as a random sample of environments and entries as fixed effects.

The statistical model used for the analysis of variance for a fullsib progeny trial for one location was:

 $Y_{ij} = \mu + R_i + G_j + e_{ij}$ 

where

Y<sub>ij</sub> = the observed value of the j<sup>th</sup> genotype in the i<sup>th</sup> replication;

 $\mu$  = the overall mean;  $R_i$  = the effect of the i<sup>th</sup> replication;  $G_j$  = the effect of the j<sup>th</sup> genotype; and  $e_{ij}$  = the experimental error associated with the ij<sup>th</sup> observation.

The following model was used for the full-sib progeny trial combined over locations:

 $Y_{ijk} = \mu + L_i + (R/L)_{ij} + G_k + (GL)_{ik} + e_{ijk} ,$ with i = 1, 2, 3; j = 1, 2; k = 1, 2, ..., 136; where  $Y_{ijk} = \text{the observed value of the } k^{th} \text{ genotype in the } j^{th}$ replication at the i<sup>th</sup> location;  $\mu = \text{the overall mean};$  $L_j = \text{the effect of } i^{th} \text{ location};$  (R/L)<sub>ij</sub> = the effect of the j<sup>th</sup> replication within the i<sup>th</sup> location;

 $G_{L}$  = the effect of the k<sup>th</sup> genotype;

- (GL)<sub>ik</sub> = the effect of interaction between the k<sup>th</sup> genotype and the i<sup>th</sup> environment; and

The form of analysis of variance and the expected mean squares for yield and the other agronomic traits for one location and over locations are shown in Tables 3 and 4, respectively. The corresponding analysis of covariance and expected mean cross products for two different generations of inbreeding for the traits under study are given in Table 5. The components of variance and covariance were computed by equating either mean squares or mean cross products to their expectations and solving for the respective components of variance. The analysis of variance, therefore, provided estimates of the genotypic component  $(\sigma_{\underline{\rho}}^2)$ , the genotypic by environment interaction component  $(\sigma_{\sigma \ell}^2)$ , and the plot error component  $(\sigma_{2}^{2})$ . Correlations, heritabilities, and genetic coefficients of variation were calculated on the basis of expected values of variance and covariances. Heritability (h<sup>2</sup>) was estimated on a entry-mean basis from use of genotypic and phenotypic variances estimated from the combined analysis of variance. Heritability was expressed as a percentage. The following formula was used:

$$h^{2} = \frac{\hat{\sigma}_{g}^{2}}{\hat{\sigma}_{p}^{2}} \times 100 , \qquad (1)$$
Source	df <sup>a</sup>	Mean square	Expected mean squares
Replications	(r-1)		
Genotypes	(g-1)	M2	$\sigma_{e}^{2} + r\sigma_{g}^{2}$
Error	(r-1)(g-1)	M <sub>1</sub>	σ <sup>2</sup> e
Total	rg-1		

Table 3. Analysis of variance for experiments conducted in one location

<sup>a</sup>Where r = 2 replications and g = 136 full-sib progenies.

Table 4. Combined analysis of variance for the experiments conducted in three locations

Source	df <sup>a</sup>	Mean square	Expected mean squares
Locations (L)	(l-1)		
Replications/L	(r-1)l		
Genotypes (G)	(g-1)	M <sub>3</sub>	$\sigma_e^2 + r\sigma_{gl}^2 + rl\sigma_g^2$
GxL	(g-1)(l-1)	<sup>M</sup> 2	$\sigma_e^2 + r\sigma_{gl}^2$
Error	(r-1)(g-1)L	M <sub>1</sub>	σ <sup>2</sup> e
Total	rgl-1		

<sup>a</sup>Where l = 3 locations, r = 2 replications, and g = 136 full-sib progenies.

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Source	df	Mean product	Expected mean products <sup>a</sup>
Environment	(s-1)		
Genotypes	(g-1)	MP <sub>2</sub>	σe <sub>ij</sub> + sσg <sub>ij</sub>
Error	(s-1)(g-1)	MP <sub>1</sub>	σe <sub>ij</sub>

Table 5. Covariance analysis of combined data of two different generations of inbreeding for yield and the other agronomic traits

 $a_{\sigma e_{jj}}$  is the covariance of error for the same trait for two different generations;  $\sigma g_{ij}$  is the genotypic covariance for the same trait for two different generations of inbreeding; and i and j represent two different generations of inbreeding.

where

 $\hat{\sigma}_g^2$  = the estimated genetic component of variance for the trait under study in the given generation, and

 $\hat{\sigma}_{p}^{2}$  = the estimated phenotypic component of variance for the trait under study in the given generation.

Confidence interval for heritability  $(h^2)$  estimates were obtained as suggested by Knapp et al. (1985). An exact 90% (1- $\alpha = 0.90$ ) confidence limits were calculated for heritability.

$$1 - F_{\alpha/2}: df_2, df_3, M_3/M_2, 1 - F_{1-\alpha/2}: df_2, df_3 M_3/M_2$$
(2)

Where  $F_{1-\alpha/2}$ :  $df_2$ ,  $df_3$  and  $F_{\alpha/2}$ :  $df_2$ ,  $df_3$  denote  $(1-\alpha/2)$ th and  $(\alpha/2)$ th quartiles of an F-distribution, respectively, with  $df_2$  numerator and  $df_3$  denominator degrees of freedom which are associated to the  $M_2$  and  $M_3$  observed mean square, respectively. Values from the  $F(df_2, df_3)$  distribution were obtained by interpolation as suggested by Laubschner (1965).

Because the components of variance were estimated as linear

function of independent mean squares, the standard errors (SE) of the components of variance  $SE(\sigma_1^2)$  were calculated using the following formula (Hallauer and Miranda, 1981):

$$SE(\sigma_{1}^{2}) = \left[\frac{2}{c^{2}} \sum \left(\frac{M_{1}^{2}}{df_{1}+2}\right)\right]^{1/2}$$

where

c = coefficient of  $\sigma_{i}^{2}$  (it is a constant) in the mean square expectations;

 $M_1 = M_1, M_2, M_3, \ldots, M_n$  (mean squares); and

dfi = degrees of freedom associated with  $M_1, M_2, M_3, \ldots, M_n$ .

Least significant differences test (LSD) was calculated to compare differences between two means. The following formula was used:

LSD = 
$$t_{df,\alpha} \sqrt{2(EMS)/N}$$

where

EMS = error mean square;

- N = number of observations used in computing the entry means; and
- t = tabular t value for the appropriate level of significance ( $\alpha$ ) and degrees of freedom (df).

LSDs were calculated at the 0.05 and 0.01 levels of significance.

Yamada (1962) emphasized that if the measurements are taken from different individuals of the same genetic group, there would be no correspondence of individuals. Values of the observed value of one individual of the same genetic group in the i<sup>th</sup> generation and the observed value of one individual of the same genetic group in the j<sup>th</sup> generation are not the same. Therefore, the expected mean product for the error is expected to be zero. Because of this relation for this particular case, different individuals of the same genetic group are being considered. The genetic covariance was estimated by the following formula:

$$MP_{2} = \sigma e_{ij} + s g_{ij};$$
  
but  $MP_{1} = \sigma e_{ij} = 0;$  hence  
 $\hat{\sigma}g_{ij} = \frac{MP_{2}}{s},$  (3)

where

- s = the number of environments;
- MP<sub>1</sub> = observed mean product of error at two different generations; and
- $MP_2$  = observed mean product of genotypes for the trait under study for two different generations.

## Genetic coefficient of variance (GCV)

To determine changes in genetic variability among full-sib progenies for the traits under study with the advances of generations of inbreeding, the genetic coefficient of variation (GCV) was used. The GCV was used in making the comparison of genetic variability in various generations for each of the traits. The following formula was used to estimate the GCV and expressed in percentage:

$$GCV = \frac{\sqrt{\sigma^2}}{\overline{x}} \times 100 , \qquad (4)$$

where

- $\hat{\sigma}_{g}^{2}$  = the genetic component of variance for a given trait in any generation; and
- $\overline{X}$  = the mean of the given trait of the particular generation that  $\sigma_{\sigma}^2$  was estimated.

The degree of association between two traits is calculated by the coefficient of correlation. The coefficient of correlation "r" is used as a measure of the degree of association between either two traits in the same generation or the same trait in different generations. The coefficient of correlation between two traits may be expressed as:

$$r_{xy} = \frac{s_{(XY)} - s_{(X)}s_{(Y)}/N}{\sqrt{[s_{(X)}^{2} - (SX)^{2}/N][s_{(Y)}^{2} - (SY)^{2}/N]}};$$
 (5)

or as

$$\mathbf{r}_{\mathbf{x}\mathbf{y}} = \frac{\mathbf{COV}_{\mathbf{X}\mathbf{Y}}}{\sqrt{\sigma_{\mathbf{X}}^2 \sigma_{\mathbf{Y}}^2}} , \qquad (6)$$

where

X and Y = the traits under study;

 $COV_{XY}$  = the covariance between the two traits; and

 $\sigma_X^2$  and  $\sigma_Y^2$  = the components of variance of the two traits considered. The same relation is used to determine the correlation between the same trait in different generations where X and Y would represent different generations. The appropriate product-moment estimates of genotypic correlation ( $r_g$ ) can be obtained from the genetic components of variance and covariance for any pair of generations. Therefore, the genotypic correlation,  $r_g$ , between measurement on the same trait, but at different generations of inbreeding, can be defined as:

$$\mathbf{r}_{g_{ij}} = \frac{\sigma_{g_{ij}}}{\sqrt{\sigma_{g_i}^2 \sigma_{g_j}^2}}, \qquad (7)$$

where

 $\sigma g_{ij}$  = the genotypic covariance between measurement on the same trait at two different generations of inbreeding;  $\sigma_{g_i}^2$  and  $\sigma_{g_j}^2$  = the genetic variances of the same trait at different generation of inbreeding; and

i and j = the two different generations under study.
r is, therefore, the genotypic correlation between measurement on the
gij
same trait for two different generations of inbreeding.

The components of variance and covariance were estimated by solving the linear relationship of equating the observed to the expected mean squares and products from the respective analysis of variance and covariance. Thus, the correlations were calculated from the expectations of variances and covariances of combined analysis of mean squares and mean cross products.

To determine the correlation between generations of testing for each level of inbreeding (i.e.,  $S_0 \times S_0$ ,  $S_1 \times S_1$ ,  $S_2 \times S_2$ ,  $S_3 \times S_3$ , and  $S_4 \times S_4$ ) a set of selected and unselected lines was developed. The genotypic correlation between measurement on the same trait at different generations of inbreeding was calculated as a measure of the extent of inheritance of such traits in successive generations. Because environmental effects were assumed to be uncorrelated between generations (Miranda-Filho and Hallauer, 1978), all environmental covariances were

expected to be zero. All phenotypic covariances, therefore, were expected to be the same as genotypic covariance and estimate, as suggested by Yamada (1962), the genotypic correlation  $r_{g_{ij}}$  between measurement of the same trait at different generations of inbreeding, as shown in formula 7.

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## **RESULTS AND DISCUSSION**

Analyses of variance were computed on data from the full set of entries for each environment and combined over environments. Although every attempt was made to continue each pair of lines, some of them were lost because of nicking at flowering time, poor seed set, and diseased seed (Hallauer, 1984b). Thus, analyses of variance were recomputed for the set of 136 full-sib progenies that were common in each generation of inbreeding for this study; the 13 checks were also included in the analysis. The combined and individual analyses of variance, omitting the 20 full-sib progenies that were not continued, was for a randomized complete block design. In order to have a better estimates of genetic and phenotypic variances and covariances, heritability  $(h^2)$ , genetic coefficient of variation (GCV), genetic coefficient of correlation were obtained from analysis of variance that omitted the check entries. These analyses of variance were computed for individual locations and combined over locations for each generation. Analysis of variance and detailed agronomic data for yield and other agronomic traits are included in Tables 6 to 10.

Significant differences ( $P \leq 0.01$ ) were detected among full-sib progenies for all traits in each generation except for percentage of dropped ears in 1979 (Table 6) and percentage of root lodging in 1982 (Table 9) and 1983-1984 (Table 10). Root lodging in 1982 and 1983-1984 had significant genotype by environment interactions. In all analyses of variance, with and without checks, the individual and combined analysis of variance detected significant differences among entries for

36

		Mean squares					
		Grai	.n		Lod	ging	Dropped
Source	df	Yield	Moisture	Stand	Root	Stalk	ears
		q/ha	%	no.	م ب ۵۰ م من ۵۰ م م ب	%	••••
Locations (L)	2	119301.6	1099.9	29962.6	113356.5	171805.5	0.9
Rep/L	3	235.7	6.0	15.8	13039.0	334.7	0.5
Genotypes (G)	135	371.1**	8.4**	46.8**	1000.3**	482.7**	0.6 <sup>ns</sup>
GxL	270	162.6**	1.7*	31.1*	352.6**	187.2**	0.5 <sup>ns</sup>
Error	405	117.6	1.4	25.5	248.0	133.9	0.5
Total	815						
Mean		78.2	23.6	60.7	31.8	34.2	0.2
Maximum		98.1	27.0	70.1	67.0	56.2	1.9
Minimum		49.1	19.8	47.8	7.1	12.0	0.0
LSD (0.05)		12.3	0.0	5.7	17.8	13.1	0.8
CV (%)		13.9	5.0	8.3	49.5	33.9	332.5

Table 6.	Combined	analyses of	of variance	for si	x agronomic	c traits	for 13	6 BS10	x BS11(FR)C5	S <sub>A</sub> :	x S
	full-sib	progenies	compared i	n Exper	iments 25.	26. and	27 cor	nducted	in 1979	U	U

\* and \*\* indicate mean squares were significant at the 5 and 1% levels, respectively, ns indicates mean squares were not significant.

37

			Mean squares				
		Gra	Ĺn		Loc	lging	Dropped
Source	df	Yield	Moisture	Stand	Root	Stalk	ears
<u></u>		q /ha	%	no.		%	
Locations (L)	2	34920.6	2864.3	745.7	2016.2	14129.5	5.3
Rep/L	3	144.7	64.1	2.9	11.5	76.5	0.8
Genotypes (G)	135	411.4**	12.7**	38.0**	648.2**	199.0*	1.2**
GxL	270	177.7**	2.9 <sup>ns</sup>	17.3**	112.7 <sup>ns</sup>	167.8**	0.6 <sup>ns</sup>
Error	405	85.7	3.1	13.0	99.8	59.3	0.7
Total	815						
Mean		73.6	19.4	55 <b>.9</b>	14.1	8.4	0.3
Maximum		92.6	23.7	59.6	56.9	31.3	2.4
Minimum		47.2	16.2	40.6	1.1	1.1	0.0
LSD (0.05)		10.5	2.0	4.1	11.3	8.7	0.9
CV (%)		12.6	9.1	6.5	71.0	91.6	292.3

Table 7.	Combined analysis of variance for six agronomic traits for 136 BS10 x BS11(FR)C5 $S_1$ x	S <sub>1</sub>
	full-sib progenies compared in Experiments 25, 26, and 27 conducted in 1980	T

\* and \*\* indicate mean squares were significant at the 5 and 1% levels, respectively, ns indicates mean squares were not significant.

38

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Lodging         Dropped ears           and         Root         Stalk         ears           .        %        %            4         306.3         62988.8         21.1
Root         Stalk         ears          %        %        %           4         306.3         62988.8         21.1
4 306.3 62988.8 21.1
4 306.3 62988.8 21.1
8 58.9 743.8 2.3
0** 105.5** 774.6** 3.0**
1 <sup>ns</sup> 26.8 <sup>ns</sup> 232.9** 2.1 <sup>ns</sup>
2 23.1 115.9 1.9
.3 2.6 24.0 0.5
.6 32.5 71.8 3.6
.3 0.0 4.3 0.0
.3 5.4 12.2 1.6
.8 182.5 44.9 272.9
0 1 .3 .3 .3

Table 8.	Combined analysis of variance for six agronomic traits for 136 BS10 x BS11(FR)C5	S, x	s,
	full-sib progenies compared in Experiments 25, 26, and 27 conducted in 1981	2	2

\*\* indicates mean squares were significant at the 1% level and ns indicates mean squares were not significant.

39

				Mean s	quares		
		Gra	in		Lo	lging	Dropped
Source	df	Yield	Moisture	Stand	Root	Stalk	ears
		q/ha	%	no.		%%	
Locations (L)	2	65163.1	6732.9	6359.2	3055.2	149999.6	95.2
Rep/L	3	528.4	5.8	38.5	155.8	849.4	1.4
Genotypes (G)	135	924.5**	14.3**	92.0**	130.0 <sup>ns</sup>	753.5**	3.1*
GxL	270	280.8**	3.1**	37.2**	111.7**	389.7**	2.6**
Error	405	158.9	1.4	26.4	70.7	166.4	1.9
Total	815						
Mean		73.6	20.8	50.9	4.2	29.5	0.6
Maximum		97.8	24.5	62.6	23.7	60.5	3.5
Minimum		22.4	17.7	38.0	0.0	6.1	0.0
LSD (0.05)		14.3	1.3	5.8	9.5	14.6	1.6
CV (%)		17.1	5.6	10.1	198.3	43.7	226.4

Table 9.	Combined analysis of variance for six agronomic traits for 136 BS10 x BS11(FR)C5 S <sub>2</sub> x	S,
	full-sib progenies compared in Experiments 25, 26, and 27 conducted in 1982	J

\* and \*\* indicate mean squares were significant at the 5 and 1% levels, respectively, ns indicates mean squares were not significant.

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40

			Mean squares				
		Gra	in		Lodg	ing	Dropped
Source	df	Yield	Moisture	Stand	Root	Stalk	ears
	•	q/ha	%	no.		%	
Locations (L)	2	4434.7	3119.3	2480.8	10301.0	1278.5	62.1
Rep/L	3	3825.8	93.3	576.5	10.1	3328.8	9.4
Genotypes (G)	135	574.1**	14.8**	156.9**	109.3 <sup>ns</sup>	548.8**	2.2**
GxL	270	162.3**	5.3**	42.7**	103.8**	260.5**	2.0 <sup>ns</sup>
Error	405	100.9	3.4	23.6	33.4	133.8	1.6
Total	815						
Mean		64.8	22.0	45.2	4.5	21.4	0.6
Maximum		81.8	26.2	54.4	30.8	58.2	3.3
Minimum		13.9	18.3	24.9	0.0	1.9	0.0
LSD (0.05)		11.4	2.1	5.5	6.5	13.1	1.4
CV (%)		15.5	8.4	10.8	127.3	53.9	200.9

Table 10.	Combined analysis of variance for six agronomic traits for 136 BS10 x BS11(FR)C5 $S_4 \times S_4$	
	full-sib progenies compared in Experiments 25, 26, and 27 conducted in 1983 and 1984 $^4$	

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\*\* indicates mean squares were significant at the 1% level and ns indicates mean squares were not significant.

41

grain yield, moisture, and stalk lodging. The means listed in Tables 6 to 10 show the effects of the environments. Except for the combination of yield trials conducted in 1983-1984, the potential for high grain yields was present. A maximum yield of 98.07 q/ha was obtained (Entry 135) in 1979 and a minimum yield of 13.92 q/ha was obtained (Entry 136) in years 1983-1984. Grain moisture range was consistent among generations of testing, but the means for stand and root lodging tended to decrease with the generations of inbreeding. There were no specific trends observed for stalk lodging, and dropped ears tended to increase with generations (Tables 6 to 10). The coefficient of variation for grain yield, percentage of grain moisture, and stand were similar to those normally obtained for machine harvested trials. Average stalk lodging was greater than 20% in all generations except for the  $S_1 \times S_1$ generation in 1980. High stalk lodging contributes to greater experimental errors for grain yield and grain moisture. The coefficient of variation for dropped ears tended to reduce with the advance of generations.

Plant breeders are concerned with genetic variability because proper management of genetic diversity can produce permanent gain in the performance of the plant species. Successful selection is dependent on high heritability of the trait under selection. The gain from selection for a quantitative trait is directly proportional to its heritability. The potential for genetic improvement of a population is indicated by its genetic variance and the heritability is a measure of the ability of the plant breeder to recognize genetic differences among

individuals. The results of Tables 11 to 13 are very encouraging for selection among full-sib progenies for the trait evaluated.

The estimates of phenotypic variation  $(V_p)$ , genetic variability  $(V_g)$ , genotype by environment interaction  $(V_{g1})$ , variation due to error  $(V_p)$ , and the genetic coefficient of variation (GCV) for each generation are summarized in Table 11. For yield there was an increase in estimate of  $V_{(g)}$  until  $S_3 \times S_3$  generation; the estimate of  $V_{(g)}$  for the  $S_4 \times S_4$ generation was similar to the  $S_2 \times S_2$  generation. The estimates of  $V_{(g)}$ for grain moisture increased until the  $S_2 \propto S_2$  generation with the estimates in the  $\rm S_3\ x\ S_3$  and  $\rm S_4\ x\ S_4$  generations similar to the  $\rm S_1\ x\ S_1$ generation. There was a continued trend for an increase in the estimate of  $V_{(g)}$  for stand from the  $S_0 \times S_0$  to the  $S_4 \times S_4$  generation. The estimates of  $V_{(g)}$  for root lodging was largest for the S<sub>0</sub> x S<sub>0</sub> generation and declined in later generations. For stalk lodging the estimates of  $V_{(g)}$  were erratic among generations. The estimates of the  $V_{(g)}$  for dropped ears were relatively small for all generations with no consistent trend among generations. There were no consistent trends among generations for the estimates of  $V_{(g)}$  for root and stalk lodging and dropped ears. None of the estimates of  $V_{(g1)}$  and  $V_{(e)}$  exhibited a consistent trend among generations.

Genetic coefficients of variation (GCV) were calculated for each generation to determine the relation of the genetic variance to the mean of the full-sib progenies for each generation of inbreeding. Estimates of GCV have considerable utility in making the comparison of genetic variability, relative to the mean, among generations and traits. In this

			Parameter <sup>a</sup>		
Generation	v <sub>P</sub>	Vg	Vgl	Ve	GCV (%)
		• <u>G1</u>	ain yield (q/ha)		
$S_0 \times S_0$	61.9	34.8 ± 7.8	$22.5 \pm 8.1$	117.6 ± 8.2	7.5
$S_1 \times S_1$	68.6	$39.0 \pm 8.7$	46.0 ± 8.2	85.7 ± 6.0	8.5
$S_{2} \times S_{2}$	91.6	$69.5 \pm 11.2$	25.4 ± 6.4	82.4 ± 5.8	11.5
$S_3 \times S_3$	154.1	<b>107.3 ± 19.0</b>	$61.0 \pm 13.3$	$158.9 \pm 11.1$	14.1
$S_4 \times S_4$	95.4	$68.6 \pm 11.8$	$30.7 \pm 7.8$	$100.9 \pm 7.1$	12.8
Average	94.4	63.8	37.1	109.1	10.9
		G	rain moisture (%)	•	
So x So	1.4	$1.1 \pm 0.2$	$0.3 \pm 0.1$	1.4 ± 0.1	4.5
$S_1^{U} \times S_1^{U}$	2.1	$1.6 \pm 0.3$	$-0.1 \pm 0.1$	$3.1 \pm 0.2$	6.6
$S_2^{\perp} \times S_2^{\perp}$	2.9	$2.2 \pm 0.4$	$0.7 \pm 0.2$	$3.4 \pm 0.2$	6.0
$S_2^{\prime} \times S_2^{\prime}$	2.4	$1.9 \pm 0.3$	$0.9 \pm 0.1$	1.4 ± 0.1	6.6
$S_{L}^{3} \times S_{L}^{3}$	2.5	$1.6 \pm 0.3$	$0.9 \pm 0.3$	$3.4 \pm 0.2$	5.7
Average	2.3	1.7	0.5	2.5	5.9
		<u>s</u>	tand (plants/ha)		
So x So	7.8	2.6 ± 1.0	$2.8 \pm 1.6$	25.4 ± 1.8	2.7
$S_1^{\vee} \times S_1^{\vee}$	6.3	$3.5 \pm 0.8$	$2.2 \pm 0.9$	$13.0 \pm 0.9$	3.3
$S_2^{\perp} \times S_2^{\perp}$	7.3	5.0 ± 0.9	$-0.1 \pm 0.8$	$14.2 \pm 1.0$	4.6
S <sub>2</sub> x S <sub>2</sub>	15.3	9.1 ± 1.9	5.4 ± 1.8	26.4 ± 1.9	6.0
$S_{k}^{3} \times S_{k}^{3}$	26.2	$19.0 \pm 3.2$	9.5 ± 2.0	23.6 ± 1.7	9.7
Average	12.6	7.8	4.0	20.5	5.3

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Table 11.	Components of variance and coefficients of genetic variation for six agronomic traits evaluated for five generations of full-sib progenies of BS10 x BS11(FR)C5

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		Ro	ot lodging (%)		
So x So	166.7	107.9 ± 20.8	52.3 ± 17.4	248.0 ± 17.4	32.7
$S_1 \times S_2$	108.0	89.2 ± 13.7	6.5 ± 6.0	99.8 ± 7.0	67.1
$S_{2}^{1} \times S_{2}^{1}$	17.6	$13.1 \pm 2.2$	$1.8 \pm 1.4$	$23.1 \pm 1.6$	137.5
$S_{2}^{2} \times S_{2}^{2}$	21.7	$3.0 \pm 3.1$	$20.5 \pm 5.4$	70.7 ± 5.0	41.1
$S_{4}^{3} \times S_{4}^{3}$	27.3	$1.4 \pm 4.6$	35.2 ± 6.4	$33.4 \pm 2.9$	26.0
Average	68.3	42.9	23.3	95.0	60.9
		St	alk lodging (%)		
S <sub>o</sub> x S <sub>o</sub>	80.5	49.3 ± 10.1	26.7 ± 9.3	133.9 ± 9.4	20.5
$S_1^{\prime} \times S_1^{\prime}$	33.2	$5.2 \pm 4.9$	54.3 ± 7.5	59.3 ± 4.2	27.1
$S_{2}^{\perp} \times S_{2}^{\perp}$	129.1	90.3 ± 16.0	58.5 ± 10.8	115.9 ± 8.1	39.7
$S_{2}^{2} \times S_{2}^{2}$	125.6	60.6 ± 16.2	111.7 ± 17.7	$166.4 \pm 11.7$	26.4
$S_{\lambda}^{J} \times S_{\lambda}^{J}$	137.2	72.1 ± 18.4	63.4 ± 16.8	$133.8 \pm 11.5$	39.6
Average	101.1	55.5	52.9	121.9	30.7

## Dropped ears (%)

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Average	0.4	0.1	· 0.1	1.3	67.9
$S_4 \times S_4$	0.6	$0.1 \pm 0.1$	$0.2 \pm 0.1$	1.6 ± 0.1	38.9
<b>S</b> <sub>3</sub> x S <sub>3</sub>	0.5	$0.1 \pm 0.1$	$0.4 \pm 0.2$	<b>1.9 ± 0.2</b>	49.8
$S_{2}^{+} \times S_{2}^{+}$	0.5	$0.2 \pm 0.1$	$0.1 \pm 0.1$	1.9 ± 0.1	79.8
$S_1 \times S_1$	0.2	$0.1 \pm 0.0$	$-0.0 \pm 0.0$	$0.7 \pm 0.0$	107.3
S <sub>0</sub> x S <sub>0</sub>	0.1	$0.0 \pm 0.0$	$-0.0 \pm 0.0$	$0.5 \pm 0.0$	63.9

<sup>a</sup>Parameters are defined as follows:  $V_p$ ,  $V_g$ ,  $V_{g1}$ , and  $V_e$  are estimates of the phenotypic, genotype by location interaction, and experimental error components of variance, respectively; and GCV is estimate of genetic coefficient of variation.

45

	Generation						
Trait	s <sub>0</sub> × s <sub>0</sub>	s <sub>1</sub> x s <sub>1</sub>	s <sub>2</sub> x s <sub>2</sub>	<sup>s</sup> 3 * <sup>s</sup> 3	s <sub>4</sub> x s <sub>4</sub>	Average	
Yield (q/ha)	7.5	8.5	11.5	14.1	12.8	10.9	
Moisture (%)	4.5	6.6	6.0	6.6	5.7	5.9	
Stand (plants/ha)	2.7	3.3	4.6	6.0	9.7	5.2	
Root lodging (%)	32.7	67.1	137.5	41.1	26.0	60.9	
Stalk lodging (%)	20.5	27.1	39.7	26.4	39.6	30.7	
Dropped ears (%)	63.9	107.3	79.8	49.8	38.9	67.9	

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Table 12. Genetic coefficient of variation (%) for yield and the other agronomic traits for different generations of full-sib progenies derived from BS10(FR)C5 x BS11(FR)C5

particular case, the estimates of GCV provide a comparison of variation among full-sib progenies for different generations and for the traits compared in different environments (years). Obilana and Hallauer (1977) calculated GCV for each cycle of selection to determine the relation of the genetic variance to the mean of the progenies for each cycle. The estimates of GCV for grain yield and the other agronomic traits are given in Table 12. For grain yield, the estimates of GCV increased with generations of inbreeding; the GCV for the  $S_3 \times S_3$  generation was nearly twice the estimate for the  $S_0 \times S_0$  generation. Estimates of GCV for grain moisture were consistent among generations. For stand, there was a linear relationship between the GCV and the increasing generations of inbreeding, but the increase in GCV with generations was related to the decrease in average stand (Tables 6 to 10). GCV for root lodging was largest in the S $_2$  x S $_2$  generation (less root lodging, Table 8) and similar to the  $S_0 \times S_0$  generation in the  $S_3 \times S_3$  and  $S_4 \times S_4$  generation. For stalk lodging, the estimates of GCV did not exhibit and trend among generations. GCV for dropped ears was greatest in the  $S_1 \times S_1$  generation and declined in the later generations, but average percentage of dropped ears was relatively low in all generations (Tables 6 to 10).

Heritability is an important parameter to plant breeders because it is used as an index of the transmission of genetic factors and also because heritability measures the value of selection for a particular trait for different types of progenies. Heritabilities expressed in percentage for grain yield and other agronomic traits were estimated from the combined analysis of variance over locations for the 136 full-

sib progenies (Table 13). The estimates of heritability for the full-sib progenies were relatively high for all traits except for percentage of root lodging and dropped ears for the  $S_3 \times S_3$  and  $S_4 \times S_4$  generations. The lower estimates of heritability of root lodging and dropped ears may be explained partially by the relatively larger genotype by environment interaction  $(V_{o1})$  and the error terms  $(V_{p})$ . Eberhart et al. (1966) showed that if adequate number of plants per plot are included for progenies and enough replications and locations are used that higher heritabilities are expected. The heritability (h<sup>2</sup>) for grain yield increased with generations of inbreeding. For grain moisture,  $h^2$  was relatively constant among generations. The estimate of heritability for percentage of dropped ears in the  $S_1 \times S_1$  generation was more than twice the heritability estimate in the  $S_0 \propto S_0$  generation, but the estimates in later generations were similar to the  $S_0 \propto S_0$  generation. There was a linear relationship between generations and heritability for stand because the heritability increased with generations of inbreeding. Heritabilities of stalk lodging were more erratic among generations ranging from 15.7% for the  $S_1 \times S_1$  generation to 69.9% for the  $S_2 \times S_2$ generation. Estimates of heritability of root lodging were greater in the first three generations (64.7% to 82.6%), but only 14.0% in the  $S_3 \ge S_3$  and 5.1% in the  $S_4 \ge S_4$  generation. Heritability, as estimated in this study, includes all types of genetic effects, including additive, dominance, and epistasis. The estimates are also biased by the effects of genotype by year interactions in each of the different generations (Casler, 1982). It is important that the estimates of heritability be

Table 13. Heritability estimates (h<sup>2</sup>, %) calculated on progenies mean basis<sup>a</sup> for yield and other agronomic traits for different generations of full-sib progenies developed from BS10(FR)C5 x BS11(FR)C5

		Generation							
		s <sub>0</sub> × s <sub>0</sub>			s <sub>1</sub> × s <sub>1</sub>				
Trait	UL <sup>b</sup>	h <sup>2</sup>	LL <sup>b</sup>	UL	h <sup>2</sup>	LL			
Yield (q/ha)	65.5	56.2	43.8	65.9	56.8	44.6			
Moisture (%)	84.2	77.4	74.3	82.3	77.8	71.2			
Stand (plants/ha)	47.7	33.7	14.8	64.1	54.5	41.5			
Root lodging (%)	72.2	64.7	54.8	86.3	82.6	77.7			
Stalk lodging (%)	69.4	61.2	50.2	33.5	15.7	-8.2			
Dropped ears (%)	35.0	20.0	-5.2	56.5	46.5	2 <b>9.</b> 2			

 ${}^{2}h^{2} = V_{(g)}/[V_{(e)}/r\ell + V_{(g1)}/\ell + V_{(g)}] \times 100.$ 

 $^b\rm UL$  and LL are the exact upper limit and lower confidence limits for heritability, respectively, the  $h^2$  value is between them.

Generation											
	s <sub>2</sub> × s <sub>2</sub>			s <sub>3</sub> × s <sub>3</sub>			s <sub>4</sub> x s <sub>4</sub>				
UL	h <sup>2</sup>	LL	UL	h <sup>2</sup>	LL	UL	h <sup>2</sup>	LL	Average		
80.9	75.8	68.9	76.0	69.6	61.0	77.7	71.7	63.7	66.0		
79.3	74.0	66.3	82.9	78.5	72.2	71.9	64.2	54.2	74.4		
74.8	68.1	59.0	68.1	59.6	48.1	78.5	72.8	65.1	57.7		
80.0	74.6	67.4	32.2	14.0	-10.4	28.6	0.05	-26.0	48.2		
76.3	69.9	61.4	59.2	48.3	33.6	64.3	52.5	26.2	49.5		
46.3	31.6	12.6	38.1	17.4	8.5	32.2	10.8	-19.7	25.3		

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interpreted with caution because they depend on the specific plant material under study, the trait under study, the types of progenies evaluated, the environmental conditions of the trials, and the experimental conditions. Data for percentages of root and stalk lodging and dropped ears usually depend on the specific environmental conditions experienced; e.g., wind storms at specific stages of plant development and infestation by the second-generation European corn borer. Variations in estimates of heritability for lodging and dropped ears tend to be greater than for grain yield, moisture, and stand. The estimates of heritability for grain yield and moisture (Table 13) were relatively consistent over generations (and years), and the estimates are consistent with other estimates reported for full-sib progenies (Lamkey and Hallauer, 1987).

The phenotypic value (P) of a particular genotype is determined by its genetic composition (G), effects of environment (E), and the interaction of genetic and environmental effects (GE); i.e., P = G + E +GE. The genetic effects are relatively fixed for a given genotype but the environment effects influence the developmental pattern of a given genotype and the effects of environment may be different; i.e., interacts with the genetic effects. When comparisons are made within one year, the response of genotypes may be influenced by seasonal differences that can occur at the different experimental sites. The analyses of variance (Tables 6 to 10) show that the genotype by environment interactions were highly significant for grain yield for each generation of testing.

The effects of the environments on mean grain yield are illustrated

in Figures 1 and 2. Variations in average grain yield within and among generations for the three experimental sites are shown in Figure 1. The expression of phenotypes for yield was influenced in the same or in opposite directions by the genetic and nongenetic factors among the three experimental sites. Information about nongenetic causes of variation were reported (Hallauer, 1979). Plant development and growth were excellent and yield potential was high at each location in 1979. But information from the trials was not good because rain accompanied by high winds caused excessive stalk lodging at each location. Furthermore, he reported that it seemed nitrogen fertilizer was not adequate at the Ankeny location (Experiment 26, environment 2). Although the trials appeared to be in excellent condition until the wind storms occurred the last week of August and middle of October, experimental errors were larger than normally expected because of excessive root and stalk lodging. In 1980, dry conditions were not ideal for testing and making pollinations in the breeding nursery, but satisfactory data were collected from yield trials and adequate seed supplies were obtained in the breeding nursery (Hallauer, 1980b). Stress conditions were evident at each location in 1981, but the type of stress was very different among experiments: drought stress at Ames (Experiment 25, environment 1); nitrogen stress at Ankeny (Experiment 26, environment 2); and disease stress (anthracnose) at Martinsburg (Experiment 27, environment 3) (Hallauer, 1981b). In 1982, the trials at Ames (environment 1) and Columbia (environment 2) were good whereas at Martinsburg (environment 3) the trial was seriously affected by disease, primarily eyespot and anthrac-



Figure 1. Variations in average yield within and among generations for the three experimental sites



Figure 2. Differential expression of the environment and its influence in yield for the different generations of inbreeding

nose. Plant and kernel development at Martinsburg were poor, suggesting premature death. Because of early plant death and environmental conditions before harvest, the incidence of stalk lodging also was very serious at Martinsburg in 1982. Stalk and root deterioration were some of the worst ever experienced in Iowa yield trials (Hallauer, 1982). In 1983, data were obtained at only one location (Ames) because of heat and drought stress (Hallauer, 1983). The growing conditions for 1984 were extremely variable. The growing season was one of extreme, ranging from too wet in the early spring to too dry in July and August and from cool conditions in April and May to hot conditions in August and early September. The variable weather patterns affected planting and harvesting operations, and, consequently, it affected the yields realized in 1984 (Hallauer et al., 1984). It seems that the most consistent site for experimental yield trials was location 1 (Ames) (Figure 2). Although there was a decline in yield for the year 1982, it was consistent with the year 1984 where the location 2 was the same as year 1983 (Ames). Location 2 (Ankeny) seems to have a greater influence on phenotype expression. Location 3 was a combination of Martinsburg, Iowa, and Columbia, Missouri. This brief description of the seasonal conditions of the trials within each generation provides information on the variation in yield among test sites and generations (Figures 1 and 2) and the significant interactions of full-sib progenies with environments (Tables 6 to 10).

Lonnquist (1951) stated that the development of an ideal genotype is virtually impossible without some type of recurrent selection to

gradually increase the frequency of desirable genotypes; it is more important when the large number of loci involved with yield, standability and resistance to diseases and insects are considered. Comstock (1977) suggested that an optimum procedure for synthesis of such ideal genotypes is not obvious in all details. However, because phenotypic value in agricultural species depends on quantitative traits (traits that are governed by a large number of loci with small effects inherited in a multifactorial fashion and influenced largely by the environmental factors) it seems that recurrent selection will be required. Hallauer and Eberhart (1970) proposed reciprocal full-sib selection to emphasize selection for nonadditive genetic effects, as well as the additive effects. Basically, reciprocal full-sib selection is an interpopulation recurrent selection scheme that evaluates and selects among full-sib progenies generated from crossing two populations. The primary objective of the procedure is to select high-yielding, single-cross hybrids. Since selection is among pairs of genotypes, primary interest is the performance of specific combinations. Thus, selection for nonadditive effects for yield among a pair of genotypes will be maximized (Hallauer, 1967a).

The results of reciprocal full-sib selection are summarized in Table 14. The 136 full-sib progenies for the five generations did not change significantly in yielding ability as inbreeding progressed. There were significant differences among years (and generations) because of the relative yield levels of the environments within years. Six hybrid checks (three single crosses and three double crosses) were included in

<u></u>		Years or generations							
Entry <sup>a</sup>	1979 (S <sub>0</sub> x S <sub>0</sub> )	1980 (S <sub>1</sub> x S <sub>1</sub> )	1981 (S <sub>2</sub> x S <sub>2</sub> )	1982 (S <sub>3</sub> x S <sub>3</sub> )	1983-84 (S <sub>4</sub> x S <sub>4</sub> )	Average			
			q/1	na					
BS10C0	60.1	55.4	55.9	65.8	51.2	57.7			
BS11C0	62.8	53.2	49.5	60.8	52.4	55.7			
CO	61.5	54.3	52.7	63.3	51.8	56.7			
BS10Cn	63.6	65.7	60.6	64.0	59.6	62.7			
BS11Cn	69.6	59.1	53.0	61.6	57.5	60.2			
Cn	66.6	. 62.4	56.8	62.8	58.6	61.4			
BS10C0 x BS11C0	69.4	67.5	60.2	65 <b>.9</b>	60.5	64.7			
BS10Cn x BS11Cn	81.4	80.4	70.4	82.1	78.8	78.6			
B37 x Oh43	84.4	77.4	65.5	71.3	63.3	72.4			
B45 x CI31A	84.9	70.4	72.7	68.3	53.9	70.0			
B14 x B45	68.2	73.6	62.6	72.8	50.1	65.5			
$\overline{\text{sc}}$ (3) <sup>b</sup>	79.2	73.9	67.0	70.8	55.8	69.3			

Table 14. Mean grain yield (q/ha) for the 136 BS10(FR)C5 by BS11(FR)C5 full-sib progenies, populations, population crosses, and check entries included for each generation of evaluation in years 1979 to 1983-84 (different generations)

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AES704	69.6	62.5	63.7	69.9	56.3	64.4
IA5115	69.8	66.5	67.0	67.0	56.5	65.3
IA5116	85.1	72.8	62.7	71.7	64.7	71.4
DC (3)	74.9	67.3	64.4	69.5	59.2	67.1
Farmers entry	96.8	87.4	86.4	81.3	73.5	85.1
Overall mean	75.7	70.4	65.4	70.8	62.6	69.0
Mean checks (6)	77.0	70.5	65.7	70.2	57.5	68.2
Full-sib progenies (136)	78.2	73.6	72.7	73.6	64.8	72.6
Five best full-sib (5)	95.8	89.0	90.3	94.6	80.1	89.9

 $a_{\overline{CO}}$  = mean of the populations per se before selection;  $\overline{Cn}$  = mean of the populations per se after selection;  $\overline{SC}$  = mean of the three single crosses;  $\overline{DC}$  = mean of the three double crosses; and n = five for years 1979-81 and six for years 1982-84 for both populations per se and population crosses.

<sup>b</sup>Number in parentheses indicate number of entries included in mean.

all trials conducted for each generation. Average yields of the six check hybrids for each generation provide an estimate of yield potential for each generation of testing (Table 14). Relative to the average yield of the checks, the differences between average yield of checks and full-sib progenies were 1.2, 3.1, 7.0, 3.4, 7.3 q/ha for the  $S_0 \times S_0$ ,  $S_1 \times S_1$ ,  $S_2 \times S_2$ ,  $S_3 \times S_3$ , and  $S_4 \times S_4$  generation full-sib progenies, respectively. Except for the 1981 and 1983-84 comparisons of full-sib progenies vs. checks, the differences were very consistent among generations. The mean of the six checks in 1981 seems to be underestimated based on comparisons between full-sib progeny means and farmer check entry.

The original and advanced cycles of selection of the two populations were included to monitor response to selection in BS10 and BS11 and the population cross (Table 1). Yield response was good in both populations per se and their population crosses (Table 14). Yield increased 5.0 q/ha for BS10 and 4.4 q/ha for BS11; the gain of BS10Cn relative to BS10C0 was 8.7% and 8.1% for BS11Cn relative to BS11C0. Response to selection in the population per se is an estimate of indirect response with reciprocal full-sib selection. Hallauer and Miranda (1981) pointed out that any maize breeding program include three phases: one of the phases of recurrent selection is the improvement of the germplasm chosen. It is evident that full-sib reciprocal recurrent selection has accomplished this objective. It is important also that the breeder conducting reciprocal full-sib recurrent selection not only be concerned with the increase of the population means per se but also with the increase of

the population cross.

Another phase of any maize breeding plan is the development of lines for use as parent stocks in production of single cross hybrids and development of improved varieties, synthetics, and composites (Hallauer and Miranda, 1981). The data in Table 14 show that the population cross of the improved population may be used directly as a commercial variety. The BS10Cn x BS11Cn cross yielded 13.9 q/ha more than the BS10C0 x BS11CO cross, which is a 21.5% gain in grain yield after five and six cycles of reciprocal full-sib selection. Average yield of the Cn x Cn population cross over years was 10.4 q/ha (15.3%) greater than the average yield of six checks over years. The CO x CO population cross yielded 3.5 q/ha (5.4%) less than the average of six check hybrids. Hence, reciprocal full-sib selection improved the population cross mean 20.4% relative to the mean at the check hybrids. The Cn x Cn population cross also exceeded the average yield over years of each of the six check hybrids. The direct response to reciprocal full-sib selection was greater (as expected) than the indirect response, but improvement was realized in all instances.

Progress from full-sib reciprocal recurrent selection was effective relative to the heterosis expressed in the population cross (Table 14). Heterosis of BS10CO x BS11CO relative to midparent was 14.1%. Midparent heterosis of the Cn x Cn population cross was 28.0%. The expression of heterosis requires differences in gene frequency and some level of dominance. It does not seem level of dominance would change significantly with only five or six cycles of selection. Therefore, gene frequency

changes must have changed in a complimentary manner for the level of heterosis to increase from the CO  $\times$  CO to Cn  $\times$  Cn.

Means for grain yield for the set of checks, the 136 full-sib progenies, and the five highest yielding full-sib progenies for each year for the whole period of study are listed in the last three rows of Table 14. Average yield for the five years was 72.6 q/ha for the 136 full-sib progenies, 89.9 q/ha for the five highest yielding full-sib progenies. The average difference between the mean of 136 and five best yielding full-sib progenies was 17.3 q/ha, which was consistent across each year or generation. The average yield for the three single-cross checks was 69.3 q/ha and 67.1 q/ha for the three double-cross hybrids (Table 14). Average yield of the six common hybrids was 68.2 q/ha. The mean yield of the five best full-sib progenies was 4.8 q/ha more than the best check (Farmer entry) that was included in all trials. Reciprocal full-sib selection had identified crosses that were either equal to or superior to the check hybrids for yield.

These results included in Table 14 suggest favorable alleles for grain yield were in the populations. Effective selection within and between the populations should provide materials that are useful to the breeders. It seems that recurrent selection will ensure genetic advance. In this study, heterosis was increased with selection and may be used directly for commercial purposes.

The results of Table 15 show that there was not as much variation in grain moisture as for grain yield for the entries included in the present study. The five best full-sib progenies for grain moisture

		Years or generations							
Entry <sup>a</sup>	1979 (S <sub>0</sub> x S <sub>0</sub> )	1980 (s <sub>1</sub> x s <sub>1</sub> )	1981 (s <sub>2</sub> x s <sub>2</sub> )	1982 (s <sub>3</sub> x s <sub>3</sub> )	1983-84 (s <sub>4</sub> x s <sub>4</sub> )	Average			
			%			****			
BS10C0	23	17	25	20	21	21			
BS11C0	24	21	28	23	24	24			
<del>co</del>	24	19	27	22	23	23			
BS10Cn	23	18	24	20	22	21			
BS11Cn	24	19	26	20	23	22			
Cn	24	19	25	20	23	22			
BS10C0 x BS11C0	23	19	24	21	21	22			
BS10Cn x BS11Cn	22	18	25	20	22	21			
B37 x Oh43	24	19	26	21	20	22			
B45 x CI31A	26	21	25	21	22	23			
B14 x B45	21	18	22	19	21	20			
$\overline{SC}$ (3) <sup>b</sup>	24	19	24	20	21	22			

Table 15. Mean grain moisture (%) for the 136 BS10(FR)C5 by BS11(FR)C5 full-sib progenies, populations, population crosses, and check entries included for each generation of evaluation in years 1979 to 1983-84 (different generations)

AES704	23	17	25	20	21	21
IA5115	23	19	24	20	22	22
IA5116	23	20	24	20	22	22
DC (3)	23	19	24	20	22	22
Farmers entry	24	20	23	22	23	22
Overall mean	23	19	25	21	22	22
Mean checks (6)	23	19	24	20	21	22
Full-sib progenies (136)	24	19	25	21	22	22
Five best full-sib (5)	21	17	21	18	19	19

 $a_{\overline{CO}}$  = mean of the populations per se before selection;  $\overline{Cn}$  = mean of the populations per se after selection; SC = mean of the three single crosses; DC = mean of the three double crosses; and n = five for years 1979-81 and six for years 1982-84 for both populations per se, and population crosses.

<sup>b</sup>Number in parentheses indicate number of entries included in mean.

showed a significant reduction in comparison with the population cross and the hybrid checks. There was a small increase for stand not only in the population per se after selection but also in the population crosses (Table 16). In comparison with the checks, there was better performance for standability of the population crosses, and it was expected the performance of the five best full-sib progenies for stand would be superior to the other entries. On the average, root lodging of the population crosses was lower than for the population per se. Root lodging of the hybrid checks was lower than for the populations per se and populations crosses, but the best five full-sib progenies for root lodging showed a significant reduction in comparison with the checks (Table 17). The results show that there was a reduction (12.0%) in average stalk lodging for the population cross after selection (Table 18). The superiority of the five best full-sib progenies for stalk lodging resistance was evident in comparisons with the average stalk lodging of the hybrid checks. The five best full-sib progenies averaged 10.8% less stalk lodging than the check hybrids. There was not a significant change in dropped ears of the five best full-sib progenies compared with the check hybrids (Table 19). Incidence of dropped ears was relatively low in most instances. The results included in Tables 14-19 show there was a positive response for yield in the population cross (Table 14) and this increase in grain yield was accompanied without selection for later maturity genotypes (Table 15). Stalk lodging decreased, but there were no significant changes in root lodging and dropped ears.

Correlation coefficients imply a causal relationship. When dealing
		Years	or generatio	on		Average
Entry <sup>a</sup>	1979 (s <sub>0</sub> x s <sub>0</sub> )	1980 (s <sub>1</sub> x s <sub>1</sub> )	1981 (s <sub>2</sub> x s <sub>2</sub> )	1982 (s <sub>3</sub> x s <sub>3</sub> )	1983-84 (s <sub>4</sub> x s <sub>4</sub> )	
			plant	s/ha		
BS10C0	53.8	57.0	46.4	54.0	45.0	51.2
BS11C0	58.2	54.8	44.2	54.4	41.2	50.6
<del>co</del>	56.0	55.9	45.3	54.2	43.1	50.9
BS10Cn	61.2	56.6	46.6	55.6	44.4	52.9
BS11Cn	62.3	56.4	53.0	50.8	47.2	53.9
Cn	61.8	56.5	49.8	53.2	45.8	53.4
BS10C0 x BS11C0	60.2	55.2	49.2	49.4	46.0	52.0
BS10Cn x BS11Cn	60.4	56.2	48.8	51.4	49.2	53.2
B37 x Oh43	63.1	55.6	46.0	51.8	46.2	52.5
B45 x CI31A	60.2	56.4	52.0	49.0	45.2	52.6
B14 x B45	57.4	51.8	46.4	50.6	35.9	48.4
$\overline{\text{SC}}$ (3) <sup>2</sup>	60.2	54.6	48.1	50.5	42.4	51.2

Table 16. Mean stand (%) for the 136 BS10(FR)C5 by BS11(FR)C5 full-sib progenies, populations, population crosses, and check entries included for each generation of evaluation in years 1979 to 1983-84 (different generations)

AES704	61.0	55.6	47.0	49.8	38.6	50.4
1A5115	59.4	53.2	45.6	51.2	39.4	49.8
IA5116	60.4	54.2	47.4	51.0	43.2	51.2
<u>DC</u> (3)	60.3	54.3	46.7	50.7	40.4	50.5
Farmers entry	58.8	57.4	45.2	53.2	41.6	51.2
Overall mean	59.7	55.4	47.5	51.7	43.3	51.5
Mean checks (6)	60.3	54.5	47.4	50.6	41.4	50.8
Full-sib progenies (136)	60.7	55.9	48.3	50.9	45.2	52.2
Five best full-sib (5)	66.1	59.2	52.9	58.6	53.3	58.0

 $a_{\overline{CO}}$  = mean of the populations per se before selection;  $\overline{Cn}$  = mean of the populations per se after selection; SC = mean of the three single crosses; DC = mean of the three double crosses; and n = five for years 1979-81 and six for years 1982-84 for both populations per se, and population crosses.

<sup>b</sup>Number in parentheses indicate number of entries included in mean.

		Years or generation						
Entry <sup>a</sup>	1979 (S <sub>0</sub> x S <sub>0</sub> )	1980 (s <sub>1</sub> x s <sub>1</sub> )	1981 (S <sub>2</sub> x S <sub>2</sub> )	1982 (s <sub>3</sub> x s <sub>3</sub> )	1983-84 (S <sub>4</sub> x S <sub>4</sub> )	Average		
			%					
BS10C0	18.9	11.0	0.5	0.7	0.0	6.2		
BS11C0	35.2	15.3	5.4	5.7	2.6	12.8		
<del>co</del>	27.1	13.2	3.0	3.2	1.3	9.6		
BS10Cn	20.1	7.9	0.8	6.7	9.4	9.0		
BS11Cn	28.7	14.6	2.0	3.1	4.9	10.7		
Cn	24.4	11.3	1.4	4.9	7.2	9.8		
BS10C0 x BS11C0	30.7	3.1	1.4	1.7	3.1	8.0		
BS10Cn x BS11Cn	31.4	11.7	2.0	0.4	2.7	9.6		
B37 x Oh43	16.5	2.3	0.5	2.6	0.0	4.4		
B45 x CI31A	33.0	13.3	1.1	0.8	9.8	11.6		
B14 x B45	29.3	6.3	2.8	0.0	0.0	7.7		
$\overline{\text{SC}}$ (3) <sup>b</sup>	. 26.3	7.3	1.5	1.1	3.3	7.9		

Table 17. Mean root lodging (%) for the 136 BS10(FR)C5 by BS11(FR)C5 full-sib progenies, populations, population crosses, and check entries included for each generation of evaluation in years 1979 to 1983-84 (different generations)

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AES704	19.2	12.7	0.9	0.8	1.6	7.0
1A5115	25.5	8.9	2.7	6.4	3.7	9.4
1A5116	17.1	9.8	0.8	1.2	1.5	6.1
<u>DC</u> (3)	20.6	10.5	1.5	2.8	2.3	7.5
Farmers entry	<b>21.2</b>	6.7	0.0	1.2	4.4	6.7
Overall mean	25.1	9.5	1.6	2.4	3.4	8.4
Mean checks (6)	23.4	8.9	1.5	2.0	2.8	7.7
Full-sib progenies (136)	31.8	14.1	2.6	4.2	4.5	11.4
Five best full-sib (5)	9.3	. 1.8	0.0	0.0	0.0	2.2

 $a_{\overline{CO}}$  = mean of the populations per se before selection;  $\overline{Cn}$  = mean of the populations per se after selection;  $\overline{SC}$  = mean of the three single crosses;  $\overline{DC}$  = mean of the three double crosses; and n = five for years 1979-81 and six for years 1982-84 for both populations per se, and population crosses.

<sup>b</sup>Number in parentheses indicate number of entries included in mean.

		Year	or generation	IS		· ·
Entry <sup>a</sup>	1979 (s <sub>0</sub> x s <sub>0</sub> )	1980 (s <sub>1</sub> x s <sub>1</sub> )	1981 (s <sub>2</sub> x s <sub>2</sub> )	1982 (s <sub>3</sub> x s <sub>3</sub> )	1983-84 (S <sub>4</sub> x S <sub>4</sub> )	Average
			%			
BS10C0	42.6	10.1	32.2	22.3	24.8	26.4
BS11C0	32.8	8.8	24.1	36.2	26.2	25.6
CO	37.7	9.5	28.2	29.3	25.5	26.0
BS10Cn	43.9	7.4	33.3	39.9	22.7	29.4
BS11Cn	38.0	6.0	27.7	28.6	14.2	22 <b>.9</b>
Cn	41.0	6.7	30.5	34.3	18.5	26.2
BS10C0 x BS11C0	41.8	12.1	29.7	30.6	35.3	29.9
BS11Cn x BS11Cn	24.8	5.7	21.0	24.8	13.4	17.9
B37 x Oh43	20.6	1.8	13.5	9.3	4.1	9.9
B45 x CI31A	28.3	15.2	46.2	30.4	20.1	28.0
B14 x B45	43.9	0.8	27.3	10.9	4.5	17.5
$\overline{\text{SC}}$ (3) <sup>b</sup>	30.9	5.9	29.0	16.9	9.6	18.5

Table 18. Mean stalk lodging (%) for the 136 BS10(FR)C5 by BS11(FR)C5 full-sib progenies, populations, population crosses, and check entries included for each generation of evaluation in years 1979 to 1983-84 (different generations)

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AES704	19.6	2.2	13.2	15.3	8.6	11.8
IA5115	22.7	2.3	24.5	28.2	9.4	17.4
IA5116	36.5	4.1	25.0	24.9	11.9	20.5
DC (3)	26.3	2.9	20.0	22.8	10.0	16.4
Farmers entry	14.4	4.2	2.6	10.7	11.3	8.6
Overall mean	. 31.5	6.2	24.6	24.0	15.9	20.4
Mean checks (6)	28.6	4.4	25.0	19.8	9.8	17.5
Full-sib progenies (136)	34.2	8.4	24.0	29.5	21.4	23.5
Five best full-sib (5)	14.0	1.7	5.3	9.1	3.6	6.7

 $a_{\overline{CO}}$  = mean of the populations per se before selection;  $\overline{Cn}$  = mean of the populations per se after selection;  $\overline{SC}$  = mean of the three single crosses;  $\overline{DC}$  = mean of the three double crosses; and n = five for years 1979-81 and six for years 1982-84 for both populations per se, and population crosses.

<sup>b</sup>Number in parentheses indicate number of entries included in mean.

	Years or generations						
Entry <sup>a</sup>	1979 (s <sub>0</sub> x s <sub>0</sub> )	1980 (S <sub>1</sub> x S <sub>1</sub> )	1981 (S <sub>2</sub> x S <sub>2</sub> )	1982 (s <sub>3</sub> x s <sub>3</sub> )	1983-84 (s <sub>4</sub> x s <sub>4</sub> )	Average	
			%				
BS10C0	0.0	0.4	0.5	0.6	0.0	0.3	
BS11C0	0.4	0.3	2.3	1.6	2.4	1.4	
CO	0.2	0.4	1.4	1.1	1.2	0.9	
BS10Cn	0.0	0.4	0.0	0.5	0.0	0.2	
BS11Cn	0.9	0.9	0.8	0.6	0.0	0.6	
Cn	0.5	0.7	0.4	0.6	0.0	0.4	
BS10CO x BS11CO	0.0	0.7	0.8	1.2	. 0.0	0.5	
BS10Cn x BS11Cn	0.3	0.7	0.8	1.1	0.0	0.6	
B37 x Oh43	0.7	1.4	0.0	0.0	0.0	0.4	
B45 x CI31A	0.0	0.3	0.8	0.6	1.1	0.6	
B14 x B45	0.0	0.0	0.5	0.0	0.0	0.1	
$\overline{\text{SC}}$ (3) <sup>b</sup>	0.2	0.6	Ó.4	0.2	0.4	0.4	

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Table 19.	Mean dropped ears (%) for the 136 BS10(FR)C5 by BS11(FR)C5 full-sib progenies, popula-
	tions, populations crosses, and check entries included for each generation of evaluation
	in years 1979 to 1983-84 (different generations)

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AES704	0.4	0.0	0.4	1.0	0.0	0.4
1A5115	0.0	0.0	0.4	1.2	0.0	0.3
1A5116	0.3	0.0	0.0	1.1	0.0	0.3
<u>DC</u> (3)	0.2	0.0	0.3	1.1	0.0	0.3
Farmers entry	0.7	0.3	0.0	2.0	2.2	1.0
Overall mean	0.3	0.4	0.6	0.9	0.4	0.5
Mean checks (6)	0.2	0.3	0.4	0.7	0.2	0.4
Full-sib progenies (136)	0.2	0.3	0.5	0.6	0.6	0.4
Five best full-sib (5)	0.0	0.0	0.0	0.0	0.0	0.0

 $a_{\overline{CO}}$  = mean of the populations per se before selection;  $\overline{Cn}$  = mean of the populations per se after selection;  $\overline{SC}$  = mean of the three single crosses;  $\overline{DC}$  = mean of the three double crosses; and n = five for years 1979-81 and six for years 1982-84 for both populations per se, and population crosses.

<sup>b</sup>Number in parentheses indicate number of entries included in mean.

with biological data, careful analysis should be given to have useful value. It is important that the correlations obtained are specific and apply only to the particular population of individuals under study. Falconer (1981) stated that the genetic mechanism responsible for causing a linear association between two traits may be due to pleiotropy, linkage, or both. Thus, the coefficient of correlation in some sense is indicative of the genes that are contributing to the expression of two traits. That is, if two traits have no genes in common, they are expected to be uncorrelated. Also, the coefficients of correlation have been used to some extent to indicate the degree of inheritance in traits between parent and offspring. It is expected that traits with higher heritabilities require less intensive testing and display closer genotypic correlations between early and late generations than those with lower heritabilities. Thus, the higher heritability of a trait under selection, the more effective is early selection. Falconer (1952) emphasized that a trait measured in two different environments may be considered as two distinct traits. On this basis, Eisen and Saxton (1983) considered that a genetic correlation of nearly one implies that genotype by environment variance was neglible. In contrast, a genetic correlation that is less than one means that genotype by environment interaction may be biologically important.

The estimates of genotypic coefficients of correlation between generations of testing for yield and the other agronomic traits included in this study were based on combined analyses of variance over locations and covariances over years for the 136 full-sib progenies for each

generation of inbreeding. Also, phenotypic correlation coefficients (Pearson correlation) were calculated on the same basis as the genotypic correlation coefficients. When the trait alone is considered as two different traits, each one measured at two different generations of inbreeding, the phenotypic correlation coefficients are given in Table 20. In general, higher correlations were obtained for the closer successive generations for all traits studied. These values tend to decline with the advance in the number of generations. Grain yield and moisture were the two traits with the highest coefficient of correlations. For stand, the coefficients were mainly negative between generations, when  $S_0 \times S_0$  generation was a member of the pair, but for  $S_1 \times S_1$  and more advanced generation the correlation coefficients tend to increase and to change the positive values. None of the correlations for stand, however, has practical use because of low values. For root lodging, there does not seem to be any significant trends among generations, but they tend to be relatively larger. Stalk lodging and dropped ears exhibited the same trend as shown by grain yield and moisture: the correlation coefficients decreased with the increase in number of generations from the  $S_0 \propto S_0$  generation.

Within the different generations of inbreeding, phenotypic correlation coefficients between yield and the other agronomic traits were calculated, and they are listed in Table 21. The highest estimates of the correlation coefficient were found for grain yield and grain moisture. The estimates were greater for grain yield and moisture at the  $S_2 \times S_2$  and  $S_3 \times S_3$  generations. The highest correlation between

•				Generation	ns	
Trait		s <sub>0</sub> x s <sub>0</sub>	s <sub>1</sub> × s <sub>1</sub>	s <sub>2</sub> x s <sub>2</sub>	s <sub>3</sub> × s <sub>3</sub>	s <sub>4</sub> x s <sub>4</sub>
Yield	$S_0 \times S_0$ $S_1 \times S_1$ $S_2 \times S_2$ $S_3 \times S_3$ $S_4 \times S_4$	1.00	0.49 1.00	0.36 0.40 1.00	0.25 0.31 0.58 1.00	0.19 0.31 0.29 0.44 1.00
Moisture	$ \begin{array}{c} & & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ & & & & \\ $	1.00	0.47 1.00	0.67 0.64 1.00	0.51 0.54 0.70 1.00	0.46 0.43 0.65 0.71 1.00
Stand		1.00	-0.09 1.00	-0.07 0.06 1.00	-0.04 0.11 0.16 1.00	0.09 0.01 0.14 0.24 1.00
Root lodging		1.00	0.50 1.00	0.27 0.57 1.00	0.20 0.29 0.41 1.00	0.28 0.53 0.29 0.32 1.00
Stalk lodging	$S_0 \times S_0 \\ S_1 \times S_1 \\ S_2 \times S_2 \\ S_3 \times S_3 \\ S_4 \times S_4$	1.00	0.33 1.00	0.37 0.24 1.00	0.38 0.27 0.47 1.00	0.23 0.25 0.37 0.55 1.00
Dropped ears	$S_0 \times S_0$ $S_1 \times S_1$ $S_2 \times S_2$ $S_3 \times S_3$ $S_4 \times S_4$	1.00	0.14 1.00	0.15 0.20 1.00	0.10 0.27 0.29 1.00	0.08 0.17 0.24 0.44 1.00

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Table 20. Phenotypic correlation coefficients between measurements for the same trait for two different generations of inbreeding

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	Generations						
Trait	s <sub>o</sub> × s <sub>o</sub>	s <sub>1</sub> × s <sub>1</sub>	s <sub>2</sub> × s <sub>2</sub>	s <sub>3</sub> × s <sub>3</sub>	s <sub>4</sub> x s <sub>4</sub>		
		Yie	eld (S <sub>0</sub> x S <sub>0</sub> )	)			
Moisture	0.25	0.16	0.29	0.21	0.16		
Stand	0.18	0.03	-0.03	-0.15	0.12		
Root lodging	-0.20	-0.09	0.09	0.12	0.05		
Stalk lodging	-0.48	-0.18	-0.30	-0.37	-0.20		
Dropped ears	0.01	-0.01	0.02	0.16	0.19		
		Yie	eld (S <sub>1</sub> x S <sub>1</sub> )				
Moisture	0.19	0.19	0.27	0.18	0.21		
Stand	0.10	0.22	0.03	-0.15	-0.08		
Root lodging	-0.17	-0.15	-0.10	0.02	-0.10		
Stalk lodging	-0.09	-0.22	-0.00	-0.19	-0.07		
Dropped ears	-0.03	0.08	0.04	0.02	-0.01		
		Yie	1d (S <sub>2</sub> x S <sub>2</sub> )				
Moisture	0.28	0.22	0.34	0.34	0.33		
Stand	0.06	0.03	0.28	0.00	-0.03		
Root lodging	0.04	0.04	0.14	0.15	0.05		
Stalk lodging	-0.12	0.08	-0.44	-0.32	-0.16		
Dropped ears	0.08	0.00	0.04	-0.02	0.03		
		Yie	1d (S <sub>3</sub> x S <sub>3</sub> )				
Moisture	0.13	0.17	0.33	0.38	0.35		
Stand	0.20	0.04	0.08	0.15	0.11		
Root lodging	-0.03	-0.10	0.06	-0.01	-0.00		
Stalk lodging	-0.12	0.15	-0.25	-0.29	-0.09		
Dropped ears	0.05	-0.14	-0.08	-0.01	0.08		
		Yie	1d (S <sub>4</sub> x S <sub>4</sub> )				
Moisture	0.15	0.07	0.08	0.06	0.09		
Stand	0.11	-0.01	0.09	-0.09	0.33		
Root lodging	-0.04	-0.10	0.04	0.00	-0.21		
Stalk lodging	-0.10	-0.02	-0.09	-0.13	-0.16		
	0.05	0.02	-0.03	0.07	0.02		

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Table 21. Phenotypic correlation coefficients of yield with the other agronomic traits at different generations of inbreeding

stand and grain yield was at the  $S_4 \times S_4$  generation for both traits. The correlations between grain yield and root lodging were erratic. Correlations between grain yield and stalk lodging were usually low and negative. Dropped ears did now show any definite trend, and the correlation coefficients were low and of different sign.

None of the correlations between traits within the five generations was large enough to have predictive value in selection programs. None of the agronomic traits had a significant effect on yield that was predictable for use in determining grain yield. Although none of the correlations was large, the trends of the correlations are those expected for measuring harvestable yield. Grain yield tends to increase with later maturity (higher grain moisture), and the correlations between grain yield and grain moisture were always positive (Table 21). Grain moisture needs to be considered in selection programs, or the materials under selection will mature later. Root and stalk lodging tended to have negative correlations with grain yield. For machine harvested experimental plots greater yield losses are associated with greater root and stalk lodging.

Special consideration needs to be given to the genotypic correlations because of their importance on early testing as predictors of performance in later generations. It is more relevant when the method produced by Hallauer (1967a) and Lonnquist and Williams (1967) for obtaining single-cross hybrids from full-sib families is considered. The results summarized in Table 22 are in agreement with the expectations; the highest genotypic correlation coefficients were between the closer

			Generations		
Generations	s <sub>o</sub> × s <sub>o</sub>	s <sub>1</sub> × s <sub>1</sub>	s <sub>2</sub> x s <sub>2</sub>	s <sub>3</sub> × s <sub>3</sub>	s <sub>4</sub> x s <sub>4</sub>
S <sub>O</sub> x S <sub>O</sub>	1.00	0.87	0.55	0.41	0.31
S <sub>1</sub> x S <sub>1</sub>		1.00	0.61	0.50	0.48
$S_{2} \times S_{2}$			1.00	0.79	0.39
$S_3 \times S_3$				1.00	0.63
$S_4 \times S_4$					1.00

Table 22. Genotypic correlations for yield between different generations of inbreeding for 136 full-sib progenies

generations. The greater the distance between generations, the lower genotypic correlation coefficient. Usually, the  $S_0 \propto S_0$  full-sib progenies are tested (Hallauer, 1982). The superior 20 families are determined, based on evaluation trials, and the  $S_1$  progenies of the superior performing  $S_0 \times S_0$  full-sib progenies are intermated within each population to form the next cycle population for further testing and selection. The correlations listed in Table 22 show that the highest genotypic correlation coefficient for yield at different stages of inbreeding was achieved between yield of  $S_0 \ge S_0$  full-sib progenies and yield of  $S_1 \times S_1$  full-sib progenies (r<sub>g</sub> = 0.87). It seems that the use of reciprocal full-sib recurrent selection, as described by Hallauer (1982), is of practical value. Miranda-Filho and Hallauer (1978) reported that when only one population is considered the genetic correlations showed that selection among  $S_0$  plants assures the best performance of  $S_1$  progenies but not necessarily the best performing  $S_0 \ge S_0$  and  $S_1 \ge S_0$ S1 full-sib families. But, when Miranda-Filho et al. (1982) considered

two populations, they reported that selection among  $S_0 \times S_0$  full-sib progenies, based on replicated trials, was very effective for identifying superior  $S_1 \times S_1$  crosses. Although Miranda-Filho et al. (1982) in their evaluation of the potential of full-sib reciprocal recurrent selection did not consider the environmental effects, the correlations of the Table 22 for yield are in perfect agreement with their conclusion. Therefore, it may be concluded that full-sib reciprocal recurrent selection is a workable method for identifying superior combinations of fullsib progenies which are assumed to carry either a large number of superior genes, or major genes for yield, standability, drought tolerance, root development, and other traits that contribute to vigorous plant development and high yield.

In the development of inbred lines, it is expected that the parentoffspring correlations will increase as homozygosity is approached and the effects of dominance and epistasis are reduded. Furthermore, when genetic differences are primarily due to additive effects higher correlations among generations of inbreeding are expected because the additive effects predict the expected genotypic mean of the next generation. In this particular study of full-sib reciprocal recurrent selection, the breeder is concerned with the production of full-sib progenies. Variation among full-sib progenies includes both additive and nonadditive effects, but nonadditive effects, primarily dominance, are of primary importance in the expression of heterosis. Kempthorne (1957) showed that the variance among full-sib family means is expected to be  $(\frac{1+F}{2})\sigma_A^2 +$  $(\frac{1+F}{2})^2\sigma_D^2$  for arbitrary levels of inbreeding and considering only

additive and dominance effects. The associations between generations that succeed one another had greater genetic correlations than generations of full-sib progenies developed from lines having greater differences in levels of inbreeding. If F = 0, the covariance of full-sibs is  $(1/2)\sigma_A^2 + (1/4)\sigma_D^2$ . Similarly, if F is increased to 0.5, the covariance among full-sib is  $(3/4)\sigma_A^2 + (9/16)\sigma_D^2$ . At near homozygosity (F = 1), the covariance of full-sib progenies is the total genetic variance,  $\sigma_A^2 + \sigma_D^2$ . Miranda-Filho and Hallauer (1978) and Miranda-Filho et al. (1982) concluded that the level of dominance effects more strongly affected the correlation and regression coefficients than does the structure of population. The coefficients of the components of  $\sigma_A^2$  and  $\sigma_D^2$  are more similar for succeeding generations; e.g.,  $S_0 \propto S_0 vs S_1 \times S_1$  are more similar than  $S_0 \propto S_0 vs S_4 \times S_4$ .

Rutledge et al. (1973) emphasized that the nature of genetic correlations is complex: pleiotropy, linkage disequilibrium, and change in gene frequencies with selection may contribute to the errors in estimation of genetic correlations. In this particular case where full-sib progenies were produced and evaluated each generation of inbreeding, the genetic mechanisms responsible for causing a linear association between either two traits or the same trait in different generations may be explained by some reasons other than only pleiotropy or linkage. Cockerham (1956) and Kempthorne (1954) showed that the covariance between relatives, where one is a descendent of the other, were unaffected by linkage.

Experimental results often do not provide clear evidence in support of early generation testing as a good predictor of relative performance

in later generations. In general, the  $S_0^{}$ ,  $S_1^{}$ , and  $S_2^{}$  generations are considered as early generations in hybrid breeding program. Sprague (1946) stated that if the frequency of genes governing desirable agronomic trait is sufficiently high, early testing of  $S_0$  or  $S_1$  lines will provide a better sample of material in which to inbreed than a more random sample from the same population. Russell and Machado (1978) pointed out that the identification of lines with high hybrid performance will have to be verified by thorough evaluation of testcrosses, which can be started as early as the  $S_3$  generation, perhaps as early as the  $S_2$  in some situations, and certainly not later than the  $S_4$ . The results of this study do not provide a clear answer to the question of whether selection in early generations of testing should be practiced nor whether selection should emphasize visual selection in early generations with testing delayed until later generations. These results show that the genetic correlation might not be the most reliable index of inheritance, and less when it is used as predictor of two generations that are more distantly separated. One main difficulty is that the phenotypic values of the crosses are considered rather than their genotypic values. Adequate testing may not have separated the genetic and phenotypic effects because of genotype by environment interactions. This also may be complicated by the levels of homozygosis of the parent for the traits under study. Thus, it may cause the genetic correlation coefficients to be underestimated. The failure of the phenotypic value as a correct measure of the genotype value may be an explanation for some of the differences among studies dealing with early generation testing.

results obtained for the correlations between generations for yield may be useful if there is an interest for predictive purposes in successive generations of inbreeding because suitable techniques of measurements were done. The materials under study were replicated among locations to estimate the genetic values for traits, such as yield, that are greatly influenced by environmental effects. Hence, the confounding effects of the environmental effects should have been reduced in the genotypic correlations. The change in the relative variability among full-sib progenies with inbreeding and the relative changes in the coefficients of the genetic components of variance with inbreeding probably contributed to the lower genotypic correlations of the more distant generations. The estimates of genotypic correlations for adjacent generations agreed with the theoretically expected correlations for adjacent generations; e.g.,  $S_0 \times S_0 \nabla S_1 \times S_1$  (Miranda-Filho et al., 1982).

The  $S_0$ ,  $S_1$ , and  $S_2$  generations are considered as early generations in most hybrid breeding programs. Hence, selection is done to enhance the chances of detecting superior inbred lines in later generations. But, it is important to keep in mind that the biggest difficulty in utilizing heterosis for genetic improvement is to identify the superior heterotic crosses. The results reported in Tables 23 to 33 are very encouraging for the use of reciprocal full-sib recurrent selection as a procedure for determining the potential usefulness of an inbred line in single-cross hybrids. The results of Tables 23 to 33 show that the  $S_0 \times S_0$  full-sib progenies that have predominance of desirable combination of genes are more likely to exhibit superior performance in later

				Lodging		Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha	*****	%		
135	98.07	24.00	64.35	41.38	27.73	0.00	
55	97.66	23.17	59.35	15.07	12.43	0.31	
126	96.93	25.17	63.94	23.04	30.10	0.27	
84	94.78	23.83	61.74	36.32	18.89	0.50	
81	91.39	24.67	61.54	27.85	37.12	0.90	
51	90.40	25.67	59.35	33.57	43.94	0.37	
53	90.22	23.33	60.95	26.21	26.96	0.00	
112	90.17	24.00	62.74	35.90	29.27	1.54	
151	89.80	24.17	61.90	23.95	36.51	0.00	
4	89.43	24.00	63.14	28.99	28.81	0.26	
137	88.71	23.17	62.54	54.66	20.30	0.27	
106	88.42	23.17	62.74	46.32	27.19	0.00	
144	88.12	22.00	62.74	13.22	33.31	0.36	
85	88.12	24.33	60.55	11.26	30.85	0.00	
41	88.07	25.83	61.35	19.75	28.43	0.00	
138	87.00	24.00	57.16	35.88	27.27	0.00	
132	86.79	22.83	59.95	35.28	36.59	0.60	
75	86.71	23.17	58.95	32.20	46.08	0.00	
9	86.35	22.67	61.74	18.34	32.49	0.00	
65	86.18	25.17	58.36	47.50	23.14	0.30	
Ξ	90.17	23.92	61.25	30.33	29.87	0.28	
SD (0.05)	12.3	0.0	5.7	17.8	13.1	0.8	

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Table 23. Mean for yield and the other agronomic traits for the best 20 full-sib progenies included in this study ranked by yield for the  $S_0 \times S_0$  generation

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				Lody	ging	Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha				
83	49.10	22.67	51.19	29.66	48.58	0.26	
100	57.95	23.17	58.96	61.28	40.88	0.98	
31	61.15	23.33	59.95	67.03	41.74	0.59	
124	62.93	21.50	55.77	30.12	39.81	0.00	
86	64.39	24.00	61.54	22.72	41.75	0.00	
59	64.45	23.17	61.74	51.93	41.64	0.00	
92	64.65	22.17	59.95	34.03	49.25	0.60	
7 <del>9</del>	66.19	22.67	60.15	58 <b>.8</b> 8	44.88	0.00	
146	67.81	23.17	63.14	51.68	41.38	0.89	
52	68.16	21.50	62.54	25.64	41.88	0.00	
99	68.50	24.00	60.94	19.34	41.16	0.00	
71	68.77	23.67	64.33	31.96	42.03	0.00	
122	68.87	25.00	59.55	37.58	47.20	0.00	
45	68.93	22.33	60.55	26.45	48.69	0.65	
61	69.24	22.67	62.74	27.34	40.53	0.35	
88	69.83	24.67	62.14	54.52	35.46	0.26	
107	69.84	23.50	63.14	30.63	37.27	0.32	
78	69.89	23.00	63.54	13.27	45.99	0.00	
128	69.96	26.00	59.75	46.79	39.42	0.00	
98	70.32	21.33	54.17	28.70	34.00	0.32	
Ē	66.05	23.18	60.29	37.48	42.18	0.26	
LSD (0.05)	12.3	0.9	5.7	17.8	13.1	0.8	

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Table 24. Mean for yield and the other agronomic traits for the lowest 20 full-sib progenies included in this study ranked by yield for the  $S_0 \propto S_0$  generation

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				Lody	ging	Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha		%		
51	92.57	21.00	57.96	2.94	22.18	0.98	
22	89.64	21.17	57.56	29.67	2.04	0.32	
87	89.43	21.00	57.96	8.01	6.25	0.00	
89	87.26	17.83	56.76	11.33	5.77	0.00	
77	86.49	17.67	55.57	10.04	7.30	0.00	
73	85.32	17.83	57.96	7.59	4.15	0.00	
57	84.63	21.00	54.18	29.45	11.35	0.37	
84	84.48	18.17	56.17	36.76	4.92	0.00	
7	84.39	19.50	56.17	16.45	2.44	0.00	
91	84.38	22.67	56.76	14.21	8.30	0.00	
21	84.25	20.83	54.57	20.31	13.39	0.00	
25	83.98	18.83	53.58	4.00	12.00	0.33	
138	83.96	21.33	57.96	18.55	6.29	0.37	
112	83.72	18.17	57.96	10.07	4.41	1.38	
144	83.41	17.33	57.36	16.02	3.82	1.36	
64	83.22	20.00	57.36	18.28	5.28	0.00	
90	83.13	19.00	56.56	20.96	9.54	1.78	
34	83.13	19.00	57.36	10.08	15.02	0.00	
44	83.02	19.17	54.57	12.67	17.26	0.34	
28	82.78	21.50	53.58	6.35	8.10	0.00	
x	85.16	19.56	56.40	15.21	8.49	0.36	
LSD (0.05)	10.5	2.0	4.1	11.3	8.7	0.9	

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Table 25. Mean for yield and the other agronomic traits for the best 20 full-sib progenies included in this study ranked by yield for the  $S_1 \times S_1$  generation

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				Lodg	ging	Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha		%		
83	47.21	19.67	54.57	3.99	6.47	0.73	
121	49.56	20.33	53.58	21.17	25.99	0.35	
146	53.14	19.33	50.19	7.35	31.31	0.00	
100	55.18	19.00	56.17	35.69	11.00	0.35	
59	56.96	17.83	49.99	29.26	4.41	0.00	
27	57.59	19.00	56.77	10.73	10.83	0.99	
31	57.98	20.00	57.16	47.00	5.67	1.05	
136	58.38	21.83	56.96	29.19	6.20	0.37	
10	59.09	17.83	58.56	20.94	4.48	0.00	
78	60.02	19.83	40.63	9.08	4.25	0.00	
1	60.75	17.83	52.38	27.92	7.34	0.00	
65	62.15	20.17	55.77	28.00	24.56	0.00	
71	62.88	18.33	58.95	9.96	13.11	0.00	
93	63.09	17.00	57.56	6.66	18.08	0.00	
108	64.22	18.00	56.76	3.30	21.11	0.00	
99	64.34	19.17	56.36	4.31	2.49	0.00	
80	64.56	20.00	58.96	20.31	15.42	0.00	
5	64.64	18.83	55.37	4.39	5.87	0.00	
124	64.77	16.17	55.57	43.16	5.52	0.00	
95	64.80	18.17	57.16	18.96	4.76	0.00	
x	59.57	18.92	54.97	19.07	11.44	0.19	
LSD (0.05)	10.5	2.0	4.1	11.3	8.7	0.9	

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Table 26. Mean for yield and the other agronomic traits for the lowest 20 full-sib progenies included in this study ranked by yield for the  $S_1 \times S_1$  generation

				Lodging		Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha		%~~~~		
138	90.84	26.50	48.20	3.51	16.34	0.43	
101	90.62	23.50	47.80	5.13	10.24	0.90	
87	90.36	27.00	50.79	0.00	.25.59	0.39	
9	90.03	22.50	48.60	0.00	6.63	0.00	
22	89.65	27.00	49.59	4.81	14.11	0.46	
75	89.41	25.00	52.58	0.00	22.53	0.00	
7	88.65	22.17	52.78	5.07	4.25	0.40	
102	87.72	26.67	47.21	2.79	25.55	0.00	
152	87.39	25.17	50.59	1.94	17.13	0.00	
51	86.59	27.50	48.00	2.01	33.10	0.43	
55	86.03	24.33	47.40	0.90	5.13	0.45	
113	85.65	27.17	49.99	7.34	17.65	2.44	
68	85.62	24.17	50.59	0.41	24.23	1.61	
46	85.42	22.67	50.19	2.01	15.08	0.00	
57	85.40	27.17	48.60	8.33	20.94	0.00	
130	85.37	24.67	47.80	1.94	16.57	1.25	
25	84.90	24.33	51.59	0.00	28.78	0.00	
39	84.60	26.33	47.00	1.73	19.24	1.72	
112	83.57	23.83	49.59	1.22	37.97	1.99	
120	83.54	25.33	50.79	2.75	42.00	0.77	
ĸ	87.07	25.15	49.48	2.49	20.15	0.66	
LSD (0.05)	10.3	2.1	4.3	5.4	12.2	1.6	

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Table 27. Mean for yield and the other agronomic traits for the best 20 full-sib progenies included in this study ranked by yield for the  $S_2 \times S_2$  generation

Stand M/ha 48.20 48.40 50.59 45.41 36.25	Root 5.71 0.41 2.28 1.22 3.25	Stalk 40.26 27.64 12.86 28.77	ears 0.40 0.82 1.86 0.00
M/ha 48.20 48.40 50.59 45.41 36.25	5.71 0.41 2.28 1.22 3.25	40.26 27.64 12.86 28.77	0.40 0.82 1.86 0.00
48.20 48.40 50.59 45.41 36.25	5.71 0.41 2.28 1.22 3.25	40.26 27.64 12.86 28.77	0.40 0.82 1.86 0.00
48.40 50.59 45.41 36.25	0.41 2.28 1.22 3.25	27.64 12.86 28.77	0.82 1.86 0.00
50.59 45.41 36.25	2.28 1.22 3.25	12.86 28.77	1.86 0.00
45.41 36.25	1.22 3.25	28.77	0.00
36.25	3.25		
50 50		35.51	0.49
20.29	4.78	34.08	0.00
47.80	0.00	26.76	0.00
48.20	0.00	45.91	0.00
49.00	2.61	40.23	0.00
37.64	1.47	41.26	1.48
43.02	0.00	49.60	2.75
48.20	3.10	71.76	0.43
45.21	0.42	29.03	0.00
48.80	0.00	26.97	0.00
47.40	0.00	44.71	0.00
47.00	2.12	28.69	0.00
50.99	0.00	45.62	0.00
47.21	2.31	14.34	0.00
50.19	2.36	36.08	0.39
53.58	0.00	37.47	0.38
47.18	1.60	35.88	0.45
4.3	5.4	12.2	1.6
	50.59 47.80 48.20 49.00 37.64 43.02 48.20 45.21 48.80 47.40 47.40 50.99 47.21 50.19 53.58 47.18 4.3	50.59 4.78   47.80 0.00   48.20 0.00   49.00 2.61   37.64 1.47   43.02 0.00   48.20 3.10   45.21 0.42   48.80 0.00   47.40 0.00   47.00 2.12   50.99 0.00   47.21 2.31   50.19 2.36   53.58 0.00   47.18 1.60   4.3 5.4	50.59 $4.78$ $34.08$ $47.80$ $0.00$ $26.76$ $48.20$ $0.00$ $45.91$ $49.00$ $2.61$ $40.23$ $37.64$ $1.47$ $41.26$ $43.02$ $0.00$ $49.60$ $48.20$ $3.10$ $71.76$ $45.21$ $0.42$ $29.03$ $48.80$ $0.00$ $26.97$ $47.40$ $0.00$ $44.71$ $47.00$ $2.12$ $28.69$ $50.99$ $0.00$ $45.62$ $47.21$ $2.31$ $14.34$ $50.19$ $2.36$ $36.08$ $53.58$ $0.00$ $37.47$ $47.18$ $1.60$ $35.88$ $4.3$ $5.4$ $12.2$

Table 28.	Mean for yield and the other agronomic traits for the lowest
	20 full-sib progenies included in this study ranked by
	yield for the $S_2 \times S_2$ generation

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				Lodging		Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha		%	نبار ها زند ها زند بي اي	
21	97.80	22.83	45.21	1.51	14.87	0.00	
132	96.52	22.50	53.38	1.96	28.91	0.00	
55	92.95	21.33	42.42	1.57	6.11	3.49	
2	92.93	23.00	51.39	0.79	15.30	0.58	
152	92.67	22.50	52.18	0.00	12.83	0.00	
139	91.13	22.00	54.37	0.74	36.17	0.00	
33	91.10	21.00	54.57	0.38	10.42	0.00	
80	90.48	20.83	54.17	3.85	27.15	0.00	
101	90.37	20.00	52.58	9.68	15.43	0.00	
138	90.13	21.83	52.98	0.38	19.75	0.00	
65	89.99	22.67	49.00	8.03	32.62	1.00	
102	89.80	22.83	54.17	1.45	40.44	0.00	
51	88.46	23.17	51.98	1.14	40.33	1.06	
25	88.35	21.67	52.58	0.00	34.05	0.50	
73	88.16	24.50	50.59	4.57	29.32	0.51	
114	87.75	22.50	51.39	2.90	30.13	0.98	
140	86.71	23.50	52.38	13.00	26.11	0.50	
64	86.32	20.00	51.58	9.76	16.58	0.00	
46	86.18	20.00	51.19	5.18	14.90	0.00	
<b>19</b>	86.16	22.67	54.57	3.83	32.33	0.00	
x	90.20	22.07	51.63	3.54	24.19	0.43	
LSD (0.05)	14.3	1.3	5.8	9.5	14.6	1.6	

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Table 29. Mean for yield and the other agronomic traits for the best 20 full-sib progenies included in this study ranked by yield for the  $S_3 \propto S_3$  generations

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				Lodging		Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha		%	, 	
39	22.41	19.50	46.61	5.10	24.46	0.00	
10	36.36	18.67	51.39	5.26	41.95	0.00	
124	46.60	20.67	49.40	6.56	38.54	0.55	
41	49.30	23.67	54.57	4.37	27.25	0.61	
53	52.60	17.67	47.00	0.49	37.79	2.17	
4	53.14	20.00	53.78	5.03	14.99	0.49	
24	53.28	18.83	55.37	0.77	43.02	0.00	
86	53.57	19.83	51.79	3.86	43.11	0.00	
149	53.64	23.33	48.20	2.19	31.26	0.55	
52	53.92	19.17	53.98	1.20	40.82	2.52	
14	54.20	19.83	51.98	0.42	32.97	1.02	
45	56.11	20.67	53.78	0.79	48.63	2.04	
128	56.32	19.33	54.37	7.13	53.33	0.00	
42	58.08	20.33	51.78	3.24	40.75	0.54	
27	58.52	21.83	52.78	0.00	25.07	0.00	
92	58.73	20.83	51.79	5.37	39.90	1.14	
98	59.29	19.33	47.60	7.47	33.61	0.51	
78	59.48	19.33	51.19	0.00	14.50	0.48	
97	60.07	19.17	46.21	1.55	55.46	3.10	
13	60.45	20.67	52.78	3.59	20.31	0.00	
ĸ	52.80	20.13	51.32	3.22	35.39	0.79	
LSD (0.05)	14.3	1.3	5.8	9.5	14.6	1.6	

Table 30.	Mean for yield and the other agronomic traits for the lowest
	20 full-sib progenies included in this study ranked by
	yield for the $S_3 \times S_3$ generation

				Lodging		Dropped
Entry	Yield	Moisture	Stand	Root	Stalk	ears
	q/ha	%	M/ha	ه هو به ديد دي ها بي	%	
138	81.77	23.50	46.80	4.22	13.27	0.63
33	81.04	20.67	54.37	3.89	11.54	0.00
105	79.89	23.33	45.01	1.67	29.76	0.00
38	79.26	24.17	47.60	1.78	7.79	1.78
8 <b>9</b>	78.30	23.67	47.40	2.39	18.43	0.76
113	77.51	25.33	49.39	8.92	9.59	0.58
32	77.49	21.00	44.81	0.66	10.20	0.00
46	77.30	22.00	48.80	3.71	12.37	1.76
63	77.24	20.83	50.19	3.15	18.58	0.54
65	77.15	25.83	41.43	0.76	14.22	0.78
55	76.76	23.67	45.61	1.56	6.89	1.34
30	76.72	25.00	44.22	5.51	10.52	0.00
64	76.56	21.00	48.00	0.00	15.17	0.00
134	76.49	22.50	49.20	6.22	28.55	0.00
68	75.82	20.17	47.00	2.59	24.48	0.71
37	75.71	22.17	48.20	2.38	25.02	0.59
150	75.53	23.50	43.42	3.27	24.19	0.61
101	75.32	21.17	47.80	5.76	11.53	0.00
22	75.00	25.50	47.80	14.07	26.32	0.00
152	74.66	22.67	37.44	0.00	5.43	0.00
x	77.28	22.88	46.72	3.63	16.19	0.50
LSD (0.05)	11.4	2.1	5.5	6.5	13.1	1.4

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Table 31. Mean for yield and the other agronomic traits for the best 20 full-sib progenies included in this study ranked by yield for the  $S_4 \times S_4$  generation

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				Lodging		Dropped	
Entry	Yield	Moisture	Stand	Root	Stalk	ears	
	q/ha	%	M/ha		%		
136	13.92	24.50	44.81	30.76	23.93	1.78	
39	25.33	23.00	25.49	0.00	11.08	0.00	
9	42.85	20.17	51.58	3.81	36.17	0.55	
124	44.03	22.67	35.25	8.87	31.27	1.95	
42	49.41	20.67	40.04	10.83	23.96	2.21	
66	49.92	20.33	43.42	1.11	12.34	0.63	
93	49.95	23.50	51.58	13.23	20.49	0.54	
95	50.05	20.00	44.61	7.63	20.48	0.00	
3	50.61	22.33	46.61	13.30	40.97	1.34	
99	50.91	21.00	38.84	0.61	12.43	0.00	
45	52.07	22.00	45.61	0.00	18.33	0.57	
4	52.07	22.17	48.99	2.08	7.69	0.00	
41	52.41	24.33	47.80	8.49	15.62	0.55	
115	52.53	22.33	45.61	1.78	25.33	0.69	
72	52.82	22.33	33.46	0.00	11.07	0.00	
142	54.17	22.00	39.44	3.76	58.15	0.00	
83	54.21	20.00	45.41	0.00	40.97	0.59	
47	54.65	22.67	40.63	2.72	24.44	0.58	
149	55.55	23.17	47.60	9.33	25.99	1.28	
10	55.96	19.17	41.43	0.00	5.57	0.00	
K	48.17	21.92	42.91	5.92	23.31	0.66	
LSD (0.05)	11.4	2.1	5.5	6.5	13.1	1.4	

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Table 32. Mean for yield and the other agronomic traits for the lowest 20 full-sib progenies included in this study ranked by yield for the  $S_4 \times S_4$  generation

Generations	Traits					
	Yield	Moisture	Stand	Lodging Root Stalk		Dropped ears
	q/ha	%	M/ha	%%		
S <sub>0</sub> x S <sub>0</sub>	24.1	0.7	1.0	-7.2	-12.3	0.02
$S_1 \times S_1$	25.6	0.6	1.4	-3.9	-3.0	0.17
$S_{2} \times S_{2}$	30.4	1.4	2.3	0.9	-15.7	0.21
S <sub>a</sub> xS <sub>a</sub>	37.4	1.9	0.3	0.3	-11.2	-0.36
S <sub>A</sub> x S <sub>A</sub>	29.1	1.0	0.8	-2.3	-7.1	-0.16
Average	29.3	1.1	1.2	-2.4	-9.9	-0.16

Table 33. Differences between average of the best 20 full-sib progenies and the lowest 20 full-sib progenies included in this study ranked by yield

generations. Because of the highly significant genotype by environment interaction (Tables 6 to 10), the genotypes included in this study differed in their phenotypic responses among environments. Consequently, the highest 20 full-sib progenies for yield were not always the same for all generations. But, 45% of the 20 best  $S_0 \times S_0$  entries were among the highest yielding 20 full-sib progenies in subsequent generations (Tables 23 to 32). Among the highest yield 20  $S_0 \times S_0$  full-sib progenies, four entries (4, 9, 41, and 53) appeared among the lowest 20 full-sib progenies in advanced generations of inbreeding (Tables 23 to 33). One of the  $S_0 \times S_0$  full-sib progenies identified as one of the 20 best full-sib progenies for yield (Entry 65) was included as one of the lowest entries in  $S_1 \times S_1$  generation (Tables 23 and 26) and in generations  $S_3 \times S_3$  and  $S_4 \times S_4$  was included among the 20 best full-sib progenies for yield (Tables 29 and 31). On the other hand, none of the lowest 20 full-sib progenies for yield for the  $S_0 \times S_0$  generation occurred among the 20 best full-sib progenies in the subsequent generations. The entries that showed poor performance in the earlier generations had similarly poor performance in later generations. In this particular case, it seems that there is no apparent reason to continue the inbreeding and testing of the material that the breeder is discarding in earliest generation on the basis of poor cross performance. It could be concluded that the performance of good  $S_0 \times S_0$  full-sib progenies was not always indicative of a good performance in later generations, but poor performance of a  $S_0 \times S_0$  full-sib was indicative of poor performance in later generations. These results clearly support the tenets proposed for the use of early testing; poor genotypes can be discarded based on early testing without any loss in genetic gain.

The results of the differences between the average of the best 20 full-sib progenies and the lowest 20 full-sib progenies, ranked by yield, are given in Table 33. The results show that there is an increase in the difference in grain yield for the two sets of entries (highest and lowest yielding entries) with the advance of generations of inbreeding; the same trend is observed for grain moisture. For stand, the trend was not consistent. In general, lodging was higher for the lowest yielding entries than for the highest yielding entries. Dropped ears also were higher in later generations for the lowest yielding entries. The trends for lodging and dropped ears are expected with machine harvested trials because ears on broken stalks and dropped ears were not included in measures for grain yield.

## SUMMARY AND CONCLUSIONS

Recurrent selection methods were developed to exploit the phenomenon of heterosis (interpopulation improvement) and to emphasize the additive effects of genes (intrapopulation improvement). Hallauer and Eberhart (1970) proposed a breeding method, reciprocal full-sib selection, where nonadditive genetic effects, as well as the additive effects, are utilized in selection. Hallauer (1967a) described the techniques used to produce the hybrid and selfed seed on the same plants. In cycle five (C5) of reciprocal full-sib selection, full-sib progenies for the five generations of inbreeding  $(S_0, S_1, S_2, S_3, S_4)$  were evaluated. Experiments and analyses of crosses for five generations of inbreeding were conducted to determine the relative performances of crosses at five levels of inbreeding. The objectives of this study were to: (1) estimate the variability among full-sib crosses for each generation of inbreeding to determine changes in variability among full-sib progenies with the advances of inbreeding; and (2) estimate the genetic correlations between full-sib progenies of different generations of inbreeding. The plant materials used were derived from the two 2-eared maize populations, 'Iowa Two-ear Synthetic' (BS10) and 'Pioneer Two-ear Composite' (BS11).

The individual and combined analysis of variance detected significant differences among entries for grain yield, grain moisture, and stalk lodging. The analysis of variance showed that the genotypes by environments interactions were highly significant for grain yield for each generation of testing. Hence, the expression of phenotypes for grain yield was influenced in the same or in opposite directions

by the genetic and nongenetic factors among the three experimental sites for the different generations of inbreeding considered. The coefficient of variation for grain yield, percentage of grain moisture and stand were similar to those normally obtained for machine harvest trials.

The results of this study show that reciprocal full-sib recurrent selection seems to be a useful method for identifying superior combinations of full-sib progenies which are assumed to carry either a large number of superior genes, or major genes that contribute to vigorous plant development and high yield. Reciprocal full-sib selection, as evaluated in this study, identified crosses that were either equal to or superior to check hybrids for grain yield. The average of grain yield for the population cross was higher than the average grain yield for the three single-cross and three double-cross hybrids included as checks in this study.

The genetic coefficient of variation (GCV) provided a comparison of variation among full-sib progenies for different generations and for the traits compared in different environments (years). In general, the GCV increased with the advance of generations of inbreeding for the traits considered. For grain yield, the estimates of GCV increased with the increased generations of inbreeding; the GCV for the  $S_3 \times S_3$ generation was nearly twice the estimate for the  $S_0 \times S_0$  generation. The estimates of heritability (h<sup>2</sup>) for grain yield and grain moisture were relatively consistent over generations (and years), and the estimates are consistent with other estimates reported for full-sib

progenies (Lamkey and Hallauer, 1987).

The estimates of genotypic correlations for adjacent generations agreed with the theoretically expected correlations for adjacent generations; e.g.,  $S_0 \times S_0 \vee S_1 \times S_1$ . Higher correlations were obtained for the adjacent generations for all traits studied. The highest genotypic correlations were between the closer generations. The genetic correlation decreased as distance between generations increased. The results of this study support the basic objectives of reciprocal full-sib recurrent selection, as described by Hallauer (1982). Furthermore, the experimental results of this study support the theoretical results obtained by Miranda-Filho et al. (1982) that selection among  $S_0 \times S_0$  full-sib progenies based on replicated trials is very effective for identifying superior  $S_1 \times S_1$  crosses.

On the average, the outstanding performance of a good  $S_0 \times S_0$  fullsib progeny is not always an indication of good performance in later generations, but the poor performance of a  $S_0 \times S_0$  full-sib progeny in early generations is indicative of poor performance in later generations. Early generation testing is emphasized in reciprocal full-sib recurrent selection. Information from testing full-sib progenies at five levels of inbreeding indicate that selection was effective for discriminating among better and poorer performing full-sib progenies. Poorer performing progenies were consistently poorer yielding in all generations. Early generation test information would have permitted greater selection and testing emphasis among full-sib progenies having better grain yield. Realized response, both direct and indirect, also suggest that early

generation test information was effective for identifying progenies that contributed alleles for greater grain yield.

Reciprocal full-sib recurrent selection met the objective of the improvement of the cross of two germplasm sources. The direct response to reciprocal full-sib selection was greater than the indirect response, but improvement was realized in all instances. Progress from reciprocal full-sib recurrent selection was effective relative to the heterosis expressed in the population cross. In this study, heterosis increased with selection and may be used directly for commercial purposes. Although grain yield was the trait given major emphasis in selection, positive response in selection also was realized for stalk quality and maturity.

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## ACKNOWLEDGEMENTS

This is the second opportunity that I have had to say thanks to everyone who helped me personally, academically or professionally throughout this period of my life. My chief debt is to my major profesor Dr. Arnel R. Hallauer, who provided great encouragement, assistance and advice during my studies at Iowa State University, for suggesting the thesis problem, carefully reading and assistance in the preparation of this manuscript.

I want to record my thanks to Drs. P. Hinz, A. E. Freeman, K. Lamkey and I. Carlson for their accessibility, suggestions, and being members of my committee.

I also want to record my apprecition to Dr. Ventura Gonzalez who provided the inspiration for being a plant breeder.

In undertaking this degree I was fortunate to receive financial assistance from Fondo Nacional de Investigaciones Agropecuarias (FONAIAP), Fundacion Gran Mariscal de Ayacucho (FUNDAYACUCHO), and Pioneer Overseas Corporation, for that I am deeply indebted to these organizations.

Special Thanks

To Dr. Carlos Rincones and members of Sugar Cane team for their encouragement and confidence in me.

To the people of UCRC, especially to Pastor Arthur J. Stienstra and his wife, Wilma, who faithfully provided further encouragement, and moral support.

To my former and present fellow graduate students who provided such a stimulating environment within which to work.

The author also appreciates the help afforded to him by the corn breeding staff especially to Jim Sears and Bill Akin, for assistance in the conduction of the experiments.

The arduous work of typing the thesis was done with great efficiency and good humor by Mary Lents. Special thanks to Marcie J. Lee for the assistance in punching the data into the computer. Gratitude is due also to my sister Issa and my brother Ismael, for the love, the confidence, encouragement, and concern which sustain us always.

This dissertation was possible because my family was always with me. To Migdaly, my wife, to Omar, Theo, Lete and Karpen, my sons, I want to express the most profound thanks to you for being inspiration and constant encouragement during these years at I.S.U.

This thesis is dedicated to my parents, Candida Rodriguez and Enrique Calderas, whose love and encouragement are always present.

Thanks to the Lord for being so nice to give me the opportunity to have all this wonderful people around me. Lord, give them long life, health and money to enjoy.

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