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**Estimates of genetic variability and gene action in two maize
(*Zea mays* L.) populations**

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Iowa State University, 1987

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Estimates of genetic variability and gene action
in two maize (Zea mays L.) populations

by

Geng-Chen Han

A Dissertation Submitted to the
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GENERAL INTRODUCTION

Heterosis has been exploited extensively in maize (Zea mays L.) breeding. However, the genetic basis of heterosis is still unclear. Information of genetic variances, levels of dominance, and relative importance of the genetic effects are useful in the explanation and prediction of heterosis and the utilization of maximum heterosis in commercial hybrids. Comstock and Robinson (1948, 1952) developed mating designs to estimate genetic variance and average level of dominance in maize populations. They emphasized that additive and dominance variance estimates are biased by the linkage disequilibrium and the bias will decreased as linkages are broken up in advanced random mating generations. Gardner and Lonnquist (1959) and Moll et al. (1964) estimated the genetic variances and the average levels of dominance from F₂ and the advanced random mating generations for several biparental maize populations. They concluded that linkage disequilibrium biased the estimates of genetic variances and average levels of dominance in F₂ populations. They also suggested that average levels of dominance for genes controlling maize yield are in the partial to complete dominance range. Gardner (1963) summarized the estimates of genetic parameters from maize populations and suggested that the average level of dominance for maize yield was in the partial dominance range.

Generation mean analyses have been used to estimate the genetic effects of maize yield and other traits. Gamble (1962a) estimated the genetic effects of maize yield from generation mean analysis and concluded that dominance effects were very important in maize yield.

Darrah and Hallauer (1972) estimated the genetic effects of maize yield from generation means for four types of inbred lines. They reported that dominance effects were larger and had greater frequency of significance than additive effects. The effect of linkage on the estimates of genetic effects from generation means has been discussed by several authors (Hayman, 1960, and Mather and Jinks, 1982). No report has been found in attempts to estimate the linkage bias of the estimates from generation mean analysis.

Very few results have been reported in comparing the genetic parameters in different populations. Moreno-Gonzalez and Dudley (1981) reported estimates of epistatic effects in related and unrelated maize hybrids by three different methods. They found that the estimates of genetic effects from generation mean analysis with crosses involving related lines were similar to those involving unrelated lines. Likewise, no research has been reported where heterosis, genetic variances, genetic effects, and linkage effects on the estimates were studied in the populations generated from hybrids that exhibit high and low heterosis.

The objectives of this study were to: (1) estimate the genetic parameters in the two maize populations that descended from a high performance single cross, B73 X Mo17, and a related line single cross, B73 X B84; (2) compare the genetic parameters estimated from the two populations as well as their effects on the expression of heterosis; and (3) estimate the effects of linkage on the estimates of genetic parameters by using the advanced random mating generations.

LITERATURE REVIEW

Heterosis, Level of Dominance, and Genetic Variances

The term of heterosis was coined by G. H. Shull and first proposed in 1914 (Hayes, 1952). Shull (1952) defined heterosis as the increased vigor, size, fruitfulness, speed of development, resistance to insect pests and to climatic rigors of any kind, manifested by crossbred organisms as compared with corresponding inbreds. He used the term to avoid the implication that hybrid vigor was entirely Mendelian in nature. Sprague (1953) considered that the terms hybrid vigor and heterosis were practically synonymous. Extensive reviews of heterosis are available (Sprague, 1953; Hallauer and Miranda, 1981; and Sedcole, 1981), and only a brief history of past development for the explanation of heterosis will be presented.

Several hypotheses have been proposed to account for heterosis. In general, these theories can be included into one of the two following categories: the overdominance hypothesis and the dominance hypothesis. Shull (1908) presented the first theory of heterosis, designated as the physiological stimulation or heterozygosity hypothesis. Shull's hypothesis was based on the idea that heterozygosity per se was the cause of hybrid vigor, which was essentially a non-Mendelian explanation. This theory was supported by the work of East and Hayes (1912) and Shull (1912). East (1936) suggested that if alleles had diverged slightly in function, a heterozygote might have an advantage over the homozygotes. East's suggestion established the framework of Mendelian explanation of heterozygote superiority. Hull (1945)

introduced the term "overdominance" to denote heterozygote superiority over either homozygotes at the locus level, and proposed this as the most important genetic effect in maize populations. Sprague (1953) indicated that Shull's (1908) theory of physiological stimulation was similar to Hull's (1945) theory of overdominance.

The dominance favorable growth factors hypothesis was first proposed mathematically by Bruce (1910). It assumes that dominance factors contributed by each parent of the hybrid are desirable and recessive factors are harmful. Bruce (1910) showed that the number of recessive loci in the hybrid would always be less than the average number of recessive loci in the parents. Thus a hybrid is more vigorous than its parents because it has more dominant factors. The concepts of linkage (Jones, 1917) and large number of loci (Collins, 1921) involved in heterosis made the hypothesis compatible with the observation of symmetrical F₂ distributions and the lack of superior homozygous inbred lines.

The two hypotheses are not mutually exclusive. Heterosis observed might be not only due to the loci with partial to complete dominance but also due to overdominance loci. Lonnquist and Lindsey (1964) evaluated 169 S₁ lines developed from the maize variety 'Krug'. The lines were evaluated in per se tests, in crosses to a related tester (Krug), and in crosses to an unrelated tester. Three highest and three lowest yielding lines were selected in both per se and unrelated topcross evaluations. The 12 lines were included in a diallel experiment. Testcrosses of lines selected on the basis of lines per se showed a linear trend for yield of

the High X High, High X Low, and Low X Low groups, with the High X High group being the highest yield. Testcrosses of lines selected on the basis of topcrosses to an unrelated tester showed that High X Low group had the highest yield. Lonnquist and Lindsey (1964) concluded that intercrosses of lines selected on the basis of inbred line per se resulted in a yield trend expected when additive gene action predominates and inter-crosses of lines selected on the basis of topcrosses to an unrelated tester resulted in a yield trend suggesting overdominant gene action. They further stated that selection based on inbred lines per se would be expected to emphasize additive effects rather than heterotic loci likely to be of advantage in hybrids.

Lamkey and Hallauer (1986) evaluated 24 high- and 24 low-yielding lines per se randomly selected from 'Iowa Stiff Stalk Synthetic' (BSSS) maize population. The high and low lines were crossed to produce three groups of hybrids: High X High (HH), High X Low (HL), and Low X Low (LL). There were significant differences among HH, HL, and LL hybrid group means for grain yield, and they ranked as expected under a model that assumed partial to complete dominance. Lamkey and Hallauer (1986) suggested that, on the average, overdominance was not important for yield in the BSSS population.

Estimates of genetic variance components and level of dominance are useful in the explanation of heterosis and the development of hybrid varieties. Comstock and Robinson (1948, 1952) developed three mating designs, commonly called design I, design II, and design III, to estimate genetic variance components and average level of dominance. In

design I experiment, a single random male was mated to a number of females. The variance analysis contained sums of squares due to males(m), females within males(f/m), and error. The genetic variance components were estimated according to the following relations:

$$V_m = \text{Cov}(\text{HS}) = 1/4 V_a, \text{ and}$$

$V_{f/m} = \text{Cov}(\text{FS}) - \text{Cov}(\text{HS}) = 1/4 V_a + 1/4 V_d$, where $\text{Cov}(\text{HS})$ is covariance of half-sibs, $\text{Cov}(\text{FS})$ is covariance of full-sibs, V_a is the additive genetic variance, and V_d is the variance due to dominance deviations. Design II experiment involved mating a number of males to a number of females. The variance analysis contained sums of squares due to males(m), females(f), males X females(mf), and error. Genetic variance components were estimated by:

$$V_m = V_f = \text{Cov}(\text{HS}) = 1/4 V_a, \text{ and}$$

$$V_{mf} = \text{Cov}(\text{FS}) - \text{Cov}(\text{HS}) = 1/4 V_d.$$

Design III experiment was constructed by backcrossing individual F2 plants to the two homozygous parental lines. The sources of variation in the analysis of variance were F2 males(m), F2 males X parents(mp), and error. Expected mean squares were manipulated to estimate the genetic variance components according to the following relations:

$$V_m = 1/4 V_a, \text{ and}$$

$$V_{mp} = V_d.$$

In 1948, they were primarily interested in the estimation of the average level of dominance, "a". "a" could be estimated in all three experiments by:

$$a = \left(a^2 \right)^{1/2} = \left(2V_d/V_a \right)^{1/2}.$$

Assumptions involved in the analysis as proposed by Comstock and Robinson (1952) were:

- (a). Regular diploid inheritance;
- (b). No multiple allelism;
- (c). No linkage; and
- (d). No epistasis.

Comstock and Robinson (1952) discussed the effect of linkage on the estimates of genetic variances and average level of dominance in the design III experiment. Additive genetic variance would be biased upwards if coupling phase linkages predominate and downwards if repulsion phase linkages predominate. Dominance genetic variance would be biased upwards regardless the linkage phase. Therefore, the estimate of average level of dominance would have a positive bias if repulsion phase linkage predominance.

Robinson et al. (1949) and Gardner et al. (1953) estimated additive and dominance variances by use of the design III for the F₂ populations of several maize single crosses. Estimates of average level of dominance were in the overdominance range for yield. These estimates indicated that either true overdominance or pseudo-overdominance attributable to linkage effects were present. Gardner et al. (1953) suggested that using advanced generations of the hybrids by random mating the F₂ plants can test the effect of linkage biases in the estimates of average level of dominance in F₂ populations.

In a follow-up study, Robinson et al. (1960) estimated the genetic

variance components and the average level of dominance involving the F8 generations which had been obtained by random mating from two of the F2 populations studied previously. They found that the estimates of average level of dominance in F8 were smaller than in F2 populations for yield and other traits. This indicated that linkage had an important effect on the estimates of genetic variances and average level of dominance in F2 populations.

A similar study involving F2 and F8 generations of a Corn Belt single cross, M14 X 187-2, was conducted by Gardner and Lonnquist (1959). Two samples were taken in 1953 and 1954, respectively. In sample 1, the estimates of average level of dominance for yield were in partial dominance range. Little effect of repulsion phase linkages on the estimates of average level of dominance was indicated. In sample 2, however, the estimates of average level of dominance for yield were significantly decreased from F2 to F8 generations. This suggested that the estimates of average level of dominance for F2 population were biased by the linkage effects. They suggested that on the average no more than complete dominance for genes controlling maize yield.

Moll et al. (1964), using a design III experiment, estimated the average level of dominance and the effects of linkage bias in estimation of genetic variances for two maize single crosses. Two advanced generations, F8 and F12 or F13, were involved in this experiment. The estimates of average level of dominance for yield were smaller for advanced generations than for F2 populations in both hybrids. Estimates of average level of dominance in advanced generations were not

significantly different from 1.0, the value for complete dominance, for all traits studied. They concluded that overdominance is not a prevalent kind of gene action in these two populations.

Moreno-Gonzalez et al. (1975) estimated the genetic variances and average levels of dominance for percent oil in F₂ and F₆ random-mated generations of a cross between Illinois High Oil and Illinois Low Oil strains by using design III experiment. The estimate of additive variance in the F₆ was half that in the F₂ generation. The estimate of dominance variance in F₆ did not differ from the F₂. They suggested that many loci controlling percent oil were linked in the coupling phase in the parents and genes with dominance action are either independent or some genes are dominant for low oil while others are dominant for high oil.

Enfield et al. (1969) studied the linkage effects on the estimates of genetic variance and level of dominance for pupa weight in Tribolium castaneum. They found that linkage bias was important in the estimates of genetic variances and average level of dominance for pupa weight in recent segregating generations.

Design I and design III were used by Robinson and Comstock (1955) to estimate the genetic variances and the average level of dominance of genes controlling quantitative traits in maize. The upwards bias in the estimates of average level of dominance was discussed by the authors. They suggested that the level of dominance of genes controlling maize yield was in partial to complete dominance range and overdominance existed at only a portion of the loci.

Gardner (1963) summarized the estimation of genetic parameters from maize populations. Additive variance had been shown to exist in moderate amounts for yield in all populations studied. Estimates of dominance variance suggested dominance exists at a majority of the loci involved in yield. He suggested that the average level of dominance for yield was in the partial to complete dominance range and epistatic variance seems nonsignificant in maize populations.

Eberhart et al. (1966) used combined design I and design II analyses to estimate genetic variance components in two open-pollinated varieties of maize, 'Jarvis' and 'Indian Chief'. Additive variance accounted for most of the genetic variance for yield and other characters measured in both varieties. The dominance variance was larger for yield than for other characters. Epistatic variances were found nonsignificant for yield and other traits studied in both varieties.

Hallauer (1970), using design II experiment, estimated the additive and dominance variances in both Iowa Stiff Stalk Synthetic (BSSS) and BSSS C4 populations. The average estimates of additive and dominance variance for yield were 157 ± 30 for BSSS and 174 ± 38 for BSSSC4 (g/plant). The ratio of dominance to additive variance was 1.1. Design I and design II were used by Silva and Hallauer (1975) to estimate the genetic components in the populations studied previously. Estimates of additive and dominance variance were 166 ± 24 and 184 ± 21 (g/plant), respectively. These results were similar to the study of Hallauer (1970). Silva and Hallauer (1975) suggested that the large dominance to additive variance ratio observed in these two studies was due to the

high frequency of favorable alleles in BSSS population and overdominance could exist at some loci.

Hallauer and Miranda (1981) summarized the estimates of genetic variance components and other parameters reported in the literature for maize. Most of the estimates reported were obtained by using mating designs I, II, or III developed by Comstock and Robinson (1948, 1952). The average estimates of additive and dominance variance of yield for F₂ populations developed from a cross of two inbred lines were 585.1 ± 338.5 and 451.0 ± 593.0 (g/plant), respectively. The average estimates of additive and dominance variance for synthetic populations were 225 ± 59 and 129 ± 83 (g/plant), respectively. They estimated the dominance to additive variance ratio for synthetic populations to be 0.83. Estimates of average level of dominance for yield was 1.05 in F₂ populations and 0.36 in the advanced random mated populations (F_n) of F₂ populations. Estimates of average level of dominance for F_n populations were lower than those for F₂ populations in all instances. Hallauer and Miranda (1981) suggested that partial dominance rather than complete or overdominance was predominant in the expression of gene action for maize yield.

Estimates of Genetic Effects

Several models have been developed to estimate genetic effects from generation means (Anderson and Kempthorne 1954; Hayman 1958, 1960; and Gardner and Eberhart 1966). An extensive review was given by Darrah

(1970), and only a few typical papers will be presented in this thesis.

Hayman (1958, 1960) proposed a model that permits the estimation of additive, dominance, additive X additive, additive X dominance, and dominance X dominance effects. Hayman (1958) defined the base population as the F₂ population derived from a cross of two inbred lines. If the two lines differ by any number of unlinked loci, the expected means for the parents and descendent generations in terms of genetic effects are as follows:

$$P_1 = m + d - 1/2 h + i - j + 1/4 l,$$

$$P_2 = m - d - 1/2 h + i + j + 1/4 l,$$

$$F_1 = m + 1/2 h + 1/4 l,$$

$$F_2 = m,$$

$$F_3 = m - 1/4 h + 1/16 l,$$

$$BC_1 = m + 1/2 d + 1/4 i,$$

$$BC_2 = m - 1/2 d + 1/4 i,$$

$$BS_1 = m + 1/2 d - 1/4 h + 1/4 i - 1/4 j + 1/16 l, \text{ and}$$

$$BS_2 = m - 1/2 d - 1/4 h + 1/4 i + 1/4 j + 1/16 l,$$

where "m" is the mean of F₂ population; "d" is the pooled additive effects; "h" is the pooled dominance effects; and "i", "j", and "l" are the pooled additive X additive, additive X dominance, and dominance X dominance effects, respectively. Hayman stated that if epistatic effects exist, linkage will bias the estimates of genetic effects from generation means.

Mather and Jinks (1982) described a model similar to Hayman's model (1958). They used the F generation (population of all inbred lines

derived from a cross of two inbred lines) as the reference population instead of the F2 generation. Expectations of the parents and descendent generations are as follows:

$$P1 = m + [d] + [i],$$

$$P2 = m - [d] + [i],$$

$$F1 = m + [h] + [l],$$

$$F2 = m + 1/2 [h] + 1/4 [l],$$

$$F3 = m + 1/4 [h] + 1/16 [l],$$

$$BC1 = m + 1/2 [d] + 1/2 [h] + 1/4 [i] + 1/4 [j] + 1/4 [l],$$

$$BC2 = m - 1/2 [d] + 1/2 [h] + 1/4 [i] + 1/4 [j] - 1/4 [l],$$

where "m" is the overall mean; [d], [h], [i], [j], and [l] are the pooled additive, dominance, and digenic epistatic effects, respectively.

Mather and Jinks stated that the estimates of [d] depends on the distribution of genes between the two parents. If the two parental lines differed in k genes, all favorable alleles presented in one line, and all unfavorable alleles in another line, the estimate of [d] would be the summed effects of k genes underconsideration. In general, however, some of the k genes for which the two lines differ will be present in one line and the others in another line. Mather and Jinks (1982) discribed the relationship between estimates of additive effects and the gene distributions as follows:

$$2rdS[d] = 2[d],$$

where rd is a measure of the gene distribution between two inbred lines. If all favorable alleles are present in one line, then $rd = 1$. If the favorable alleles are equally shared between the two lines, then $rd = 0$.

The estimate of $[d]$ would be zero if $rd = 0$, no matter what the additive effects are for individual loci. On the other hand, the estimate of dominant effect, $[h]$, will not be affected by the gene distribution between the parental lines. Therefore, the ratio of dominance to additive estimates, $[h]/[d]$, can be used as a measure of overdominance only in the case $rd = 1$; that is, all favorable alleles are present in one line and all unfavorable alleles in another line.

Mather and Jinks (1982) examined the effect of linkage on the estimates of parameters from generation means and emphasized that if epistasis exists, linkage will bias the estimates of all parameters except additive effect, $[d]$.

Generation mean analysis has been used to estimate the genetic effects in several experiments. Gamble (1962a, 1962b), using Hayman's model, estimated genetic effects of yield, plant height, kernel-row number, ear length, ear diameter, and 100-kernel weight for 15 crosses of maize. He reparameterized the model to follow the pattern in genetic variance analysis. The correspondence between Gamble's notations and Hayman's (1958) and Mather and Jinks' (1982) is as follow:

Gene effect	Gamble	Hayman	Mather & Jinks
mean	m	m	m
additive	a	d	$[d]$
dominance	d	h	$[h]$
additive X additive	aa	i	$[i]$
additive X dominance	ad	j	$[j]$
dominance X dominance	dd	l	$[l]$

In Gamble's experiment, dominant effects (d) of yield were positive and as large or greater than the common mean (m) in all crosses, indicating dominance effects were very important in controlling maize yield.

Additive effects were relative small compared with dominance and common mean, with 8 of 15 crosses not significantly different from zero.

Epistatic effects were found significant for some of the crosses.

Epistatic effects generally were more important than additive effects for yield. Dominance effects were also positive and play an important role for plant height, ear length, ear diameter, and kernal weight. For kernel-row number, additive effects were more important. Epistatic effects generally were small relative to dominance and additive effects for all traits except plant height.

Hughes and Hooker (1971), using Hayman's model, estimated the genetic effects for resistance to Northern leaf blight (Helminthosporium turcicum Pass.) in maize crosses produced from four resistant inbred lines, two susceptible lines, and one moderately resistant line. They concluded that leaf blight resistance in the lines was controlled by a relatively small number of genes. Additive effects were of major importance. Dominance and epistatic effects were detected, but their importance was minor relative to additive effects.

Darrah and Hallauer (1972) estimated the genetic effects of four types of maize inbred lines by Hayman's model. One of the comparisons was made between 1st cycle inbred lines, derived from open-pollinated varieties, and 2nd cycle inbred lines, selected from segregates of planned crosses or synthetic varieties. Another comparison was made

between good and poor performance inbred lines. They concluded that dominance effects were large and more important than additive effects for yield and all other traits measured except kernel-row number and 300-kernel weight. Dominance and additive effects were nearly equivalent important for kernel-row number and 300-kernel weight. Epistasis was not important for date silk and yield, but was important for plant height, ear height, and ear diameter. The 2nd cycle and poor inbred lines showed more epistasis than the 1st cycle and good lines for plant height, ear height, kernel-row number, ear length, and ear diameter. For yield, the 2nd cycle inbred lines had more epistasis than the 1st cycle inbred lines. There was little difference between good and poor lines in the occurrence of significant epistasis for yield.

Moreno-Gonzalez and Dudley (1981) studied the genetic effects in related and unrelated maize hybrids by Mather and Jinks' (1982) model. Three inbred lines derived from BSSS population and three lines related to 'Lancaster' open-pollinated variety were used to produce 15 crosses. They found that heterosis for yield and other traits measured was larger in the crosses involving unrelated lines than in crosses involving related lines. Dominance effects were the most important genetic effects controlling yield, plant height, ear height, ear length, ear diameter, and leaf area. Significant epistatic effects were found in both related and unrelated line crosses. However, the estimates of genetic effects from generation mean analysis with crosses involving related lines were similar to those of crosses involving unrelated lines.

Linkage bias on the estimates of genetic effects from generation

means have been discussed by several authors. No experiment was conducted to estimate the linkage effects on the estimates of genetic parameters from generation mean analysis.

Explanation of Dissertation Format

This dissertation is divided into two sections. Section I includes a study to evaluate the genetic variances and average level of dominance for the two maize populations that descended from two single crosses, B73 X Mo17 and B73 X B84. Section II includes a study of generation mean analysis for the two single crosses and descended generations.

Each manuscript is written in professional journal article form and will be submitted for publication. General conclusions and discussion follow Section II. References cited in the General Introduction and Literature Review are listed in "Additional References Cited" after General Conclusions. An Appendix to the dissertation follows the Additional References Cited.

SECTION I. ESTIMATION OF GENETIC VARIANCE AND AVERAGE LEVEL
OF DOMINANCE IN TWO MAIZE POPULATIONS

ABSTRACT

Information on genetic variability and level of dominance for genes controlling quantitative traits in breeding populations is useful in the development of heterosis theory and hybrid breeding strategies. The objectives of this study were: 1) to estimate the genetic variance components and average levels of dominance in two maize (Zea mays L.) populations that one descended from a high performance single-cross hybrid, B73 X Mo17, and the other from a related line single-cross hybrid, B73 X B84; 2) to compare the generation means, heterosis, and genetic variance for the two hybrids and their descended populations, and 3) to measure the effect of linkage disequilibrium on the estimates of genetic parameters in the two populations. Forty pairs of backcross progenies (BC1 and BC2) and forty S1 lines randomly sampled from each of F2 and F2 Syn5 populations were evaluated for each hybrid. Backcross progenies were analyzed by the mating design III (DIII) method. Data from backcross progenies were combined with that from S1 lines to perform the DIII and S1 combined analysis.

Heterosis and genetic variance were greater in B73 X Mo17 than in B73 X B84 for yield, ear height, ear length, and ear diameter. Heterosis for yield in B73 X Mo17 was 125.5% greater than in B73 X B84. Additive genetic variance for yield estimated for the B73 X Mo17 populations was about two and three times greater than for the B73 X B84 F2 and F2 Syn5 populations, respectively. Dominance genetic variance estimated for the B73 X Mo17 populations was also much greater than for the B73 X B84 in both F2 and F2 Syn5 populations. Estimates of average

level of dominance were in the partial to complete dominance range for all traits. There was little difference between the average levels of dominance estimated for the B73 X Mo17 and for the B73 X B84 populations. Genetic parameters estimated from DIII and S1 combined analysis were consistent with those from the DIII analyses.

Estimates of dominance variance for yield decreased from the F2 to the F2 Syn5 populations for both single crosses. Estimates of additive genetic variance of yield for the F2 populations were not significantly different from the estimates for the F2 Syn5 populations for both hybrids. This suggested that the effects of coupling and repulsion phase linkages cancelled each other in the populations. Coupling phase linkages were predominant for ear length, ear diameter, and kernel-row number in B73 X Mo17 and for ear height in B73 X B84. Repulsion phase linkages were predominant in B73 X Mo17 for ear height. The biases in the estimates of genetic parameters due to linkage disequilibrium generally were smaller in B73 X B84 than in B73 X Mo17.

INTRODUCTION

Information on genetic variability in breeding populations is of importance in making decisions for the use of efficient breeding methods and expectation of responses to selection. Estimates of average level of dominance of genes controlling a quantitative trait also are useful in the theory of heterosis and the utilization of maximum heterosis in commercial hybrids. Comstock and Robinson (1948, 1952) developed the method of mating design III to estimate genetic variance and average level of dominance in biparental populations. They emphasized that additive and dominance genetic variances are biased if the populations are in linkage disequilibrium, and the bias will decrease as linkages are broken up in advanced random mating generations.

Gardner and Lonnquist (1959) and Moll et al. (1964) estimated the genetic variances and the average levels of dominance from F₂ and advanced generations for several biparental maize (Zea mays L.) populations. They concluded that linkage disequilibrium biased the estimates of genetic variance and average level of dominance in the F₂ populations. They also suggested that average levels of dominance for genes controlling maize yield are in the partial dominance range. Enfield et al. (1969) reported that linkage had an important effect on the estimates of genetic variance and average levels of dominance in F₂ generation for pupa weight in Tribolium castanææ. Moreno-Gonzalas et al. (1975) suggested that linkage disequilibrium biased the estimates of additive genetic variance in the F₂ population for percent oil of maize, but did not bias the estimates of dominance variance. Gardner

(1963) summarized the estimates of genetic parameters from maize populations and suggested that the average level of dominance for maize yield was in the partial dominance range.

Very few results have been reported comparing the genetic parameters in the populations generated from hybrids that exhibit high and low heterosis. Moreno-Gonzalez and Dudley (1981) estimated the genetic effects in related and unrelated maize hybrids by three different methods. They concluded that heterosis for yield was greater in crosses involving unrelated lines than in crosses involving related lines. The genetic effects estimated from generation mean analysis were not associated with crosses involving related or unrelated lines.

The objectives of this study were: 1) to estimate the genetic variance components and average levels of dominance in two maize populations that one descended from a high performance single-cross hybrid, B73 X Mo17, and the other from a related line single cross, B73 X B84; 2) to compare the generation means, heterosis, and genetic variance for the two hybrids and their descended populations; and 3) to estimate the linkage effects on the estimates of genetic parameters in the two populations.

MATERIALS AND METHODS

Plant Materials and Field Procedures

Three inbred lines (B73, B84, and Mol7), two F1 single crosses (B73 X Mol7 and B73 X B84), two F2 populations of the two F1 single crosses, and two F2 synthetic 5 populations descended from the two F2 populations were used as source materials in this experiment. Both B73 and B84 were derived from 'Iowa Stiff Stalk Synthetic' (BSSS) population after five and seven cycles of half-sib recurrent selection for yield, respectively. Therefore, B73 and B84 are, to some extent, related. Mol7 was derived by pedigree selection from the cross, C103 X 38-11. B73 X Mol7 was one of the best commercial hybrids in the U.S. Corn Belt. B84 X Mol7 also has good yield performance (Russell, 1986).

The F2 populations were produced by selfing the F1 plants from each cross. The F2 synthetic 5 (F2Syn5) populations were produced by random mating 250 plants for five generations from each F2 population.

Forty unselected plants from each F2 and F2Syn5 population were used as male parents. Each plant was crossed to each of the parental inbred lines to produce 40 pairs of backcross progenies. The method of producing the backcross progenies is the mating design III described by Comstock and Robinson (1952). The F2 plants also were self-pollinated to produce S1 lines. Since insufficient seed was available for the B73 X Mol7 F2 Syn5 population, only 38 pairs of backcross progenies and their corresponding S1 lines were planted for this population. The

numbers of backcross progenies and S1 lines from each population are as follows:

Population	No. of backcrosses	No. of S1 lines
(B73XMo17)F2	80	40
(B73XMo17)F2 Syn5	76	38
(B73XB84)F2	80	40
(B73XB84)F2 Syn5	80	40
Total	316	158

The experiment, therefore, included three inbred lines, two F1 single crosses, two F2 populations, 316 backcross progenies from the F2 and F2 Syn5 populations, and 158 S1 lines from the four populations. All materials were produced at Ames, Iowa, from 1978 to 1984.

All materials except Mo17 were evaluated in three experiments. One of the experiments was conducted at the Agronomy Research Center near Ames in 1985. Two experiments were conducted in 1986, one at the Agronomy Research Center and one at the Atomic Energy Farm at Ames. Mo17 was included in the two experiments, Agronomy Research Center in 1985 and Atomic Energy Farm in 1986.

The incomplete randomized block design was used as the field design. The materials were assigned into four sets for backcross progenies and S1 lines from each population. In sets 1 to 3, each set included 80 backcross progenies and 40 S1 lines from all of the four populations. Set 4 included 76 backcross progenies, 38 S1 lines, 3 inbred lines, 2 F1 single crosses, and 2 F2 populations. Each set was subdivided into S1 and backcross subblocks to reduce the competition

between backcross progenies and S1 lines. F1 and F2 progenies were grown within the backcross subblock, and inbred lines were planted within the S1 subblock in set 4. All materials in each subblock were randomized within two replications.

In each experiment, each progeny-entry was grown in a single-row plot of 5.45 m long with 76 cm between plots. The plots were overplanted using a machine planter and then thinned to 21 plants per row for an approximate plant density of 50,000 plants per hectare. All experiments were harvested by hand.

Data were collected for days-to-silk, ear height (cm), ear length (cm), ear diameter (cm), kernel-row number, and total grain weight (yield). Ear height, ear length, ear diameter, and yield were collected in all three experiments. Days-to-silk were recorded for the two experiments conducted at the Agronomy Research Center near Ames. Kernel-row number data were collected at the two experiments conducted in 1986. All traits were taken on a plot-mean basis. The six traits were measured as follows:

1. Ear height was the distance from ground level to the node bearing the primary ear, first ear. The average height of five randomly sampled plants was recorded in cm.
2. Days-to-silk were the number of days after July 1 when 50% of the plants in a plot had visible silk.
3. Ear length was the total length in cm of 10 randomly sampled ears. The total length was divided by the number of ears measured and expressed on an ear basis.

4. Ear diameter was the average diameter in cm of 10 randomly sampled ears in a plot.

5. Kernel-row number per ear was the average number of 10 randomly sampled ears in a plot.

6. Yield was recorded as the total shelled grain weight of all harvested ears from a plot and converted to quintals per hectare.

Statistical Procedures

The experimental design used in each environment was a split-plot design with the main plots arranged in sets. The progeny types (hereafter referred to as type), backcross and S1, were main plot treatments. The entries were subplots nested within progeny types. The analysis of variance for a single set evaluated in an individual environment was conducted according to the analysis for a split-plot experiment. This analysis was then pooled over sets and combined over environments.

The analysis of variance and the expectations of mean squares pooled over sets and combined over environments is outlined in Table 1.

The following model was used to perform the analysis:

$$Y_{ijklm} = E_i + S_j + (ES)_{ij} + (R/ES)_{ijk} + T_l + (ET)_{il} + (ST)_{jl} + (EST)_{ijl} \\ + (RE/ES)_{ijkl} + (G/T/S)_{jlm} + (EG/T/S)_{ijlm} + e_{ijklm},$$

where Y_{ijklm} - the observed value of the mth genotype within the

lth type in the kth replication within the jth set
in the ith environment;

E_i - the effect of the ith environment;

S_j - the effect of the jth set;

$(ES)_{ij}$ - the effect of interaction between jth set and ith environment;

T_l - the effect of the lth type;

$(ET)_{il}$ - the effect of interaction between the lth type and the ith environment;

$(ST)_{jl}$ - the effect of interaction between the jth set and the lth type;

$(EST)_{ijl}$ - the effect of the interaction between the lth type, the jth set, and the ith environment;

$(RT/ES)_{ijkl}$ - the effect of the interaction between the lth type and the kth replication within the ijth environment-set combination; i.e., error (a);

$(G/T/S)_{ijm}$ - the effect of the mth genotype within the lth type in the jth set;

$(EG/T/S)_{ijlm}$ - the effect of interaction between ith environment and the mth genotype within the lth type in the jth set; and

e_{ijklm} - pooled experimental error; i.e., error (b).

The sum of squares due to genotypes within types within

Table 1. Form of analysis of variance, pooled over sets and combined over environments

Sources of variation	df ^a	Mean squares
Environments (E)	e-1	M11'
Sets (S)	s-1	M10
E X S	(e-1)(s-1)	M9
Replications/E X S	es(r-1)	M8
Types (T)	t-1	M7
E X T	(e-1)(t-1)	M6
S X T	(s-1)(t-1)	M5
E X S X T	(e-1)(s-1)(t-1)	M4
Error (a)	es(r-1)(t-1)	M3
Entries (G)/T/S	$s[(g_{1.} - 1) + (g_{2.} - 1)]$	M2
Backcrosses (BC)	$s(g_{1.} - 1)$	M21
S1 lines (S1)	$s(g_{2.} - 1)$	M22
E X G /T/S	$(e-1)s[(g_{1.} - 1) + (g_{2.} - 1)]$	M1
E X BC	$(e-1)s(g_{1.} - 1)$	M11
E X S1	$(e-1)s(g_{2.} - 1)$	M12
Error (b)	$es(r-1)[(g_{1.} - 1) + (g_{2.} - 1)]$	M0
BC error	$es(r-1)(g_{1.} - 1)$	M01
S1 error	$es(r-1)(g_{2.} - 1)$	M02
Total	$esr(g_{1.} + g_{2.}) - 1$	

^ae, s, r, t, and g represent the number of environments, sets, replications, types, and entries within the jth population combination for the ith type, respectively.

sets, the interactions between environments and genotypes within types within sets, and experimental error were partitioned into the components due to each population within types.

The effects of environments, sets, replications, and genotypes were considered as random in all models in which they appeared. The effect of types was considered as fixed. All analyses were conducted on plot mean basis. F-test was conducted by using appropriate mean squares for each effect.

Genetic Analysis

In this experiment, the backcross progenies in each population were produced by the method of mating design III described by Comstock and Robinson (1952). Therefore, the sums of squares due to the backcross progenies from each population were analyzed by the method of mating design III.

Data for each trait for design III progenies were analyzed by randomized complete block design for each set and pooled over sets. The experimental results also were combined over environments for each trait to perform the combined analysis of variance.

The genetic interpretation of the components of variances in design III analysis was derived by Comstock and Robinson (1952). Under the assumptions of linkage equilibrium and no epistasis, the male component of variance (V_m) is

$$V_m = \sum_i \bar{q}_i (1 - \bar{q}_i) a_i^2 / 2,$$

where V_m is the variance component among males;

q_i is the favorable allele frequency of i th locus; and

a_i is the additive gene effect of i th locus.

The male X parent component of variance (V_{mp}) is

$$V_{mp} = \sum_i q_i (1 - q_i) d_i^2,$$

where V_{mp} is the variance component due to the interaction of male X parent; q_i is allele frequency at i th locus; and d_i is dominance gene effect at i th locus.

If gene frequency is $1/2$,

$$V_m = \sum_i a_i^2 / 8 = V_a / 4, \text{ and}$$

$$V_{mp} = \sum_i d_i^2 / 4 = V_d,$$

where V_a is the additive genetic variance, V_d is the variance due to dominance deviations, and a_i and d_i are the same as defined previously. The level of dominance involved in the action of the i th pair of alleles is expressed by d_i as follows:

Level of dominance	Magnitude of d_i
No dominance	$d_i = 0$
Partial dominance	$0 < d_i < 1$
Complete dominance	$d_i = 1$
Overdominance	$d_i > 1$

An estimate of average level of dominance is

$$\bar{d} = \left(\frac{\sum_i d_i^2}{\sum_i a_i^2} \right)^{1/2} = (V_{mp} / 2V_m)^{1/2},$$

where \bar{d} is a weighted mean of d_i^2 's.

If linkage disequilibrium exists in a population, the estimates of V_m and V_{mp} will be biased due to linkage effects. V_a will be biased upwards if coupling phase linkage predominates, and downwards if repulsion phase linkage predominates. V_d will be biased upwards regardless of the predominant linkage phase. Therefore, linkage disequilibrium will contribute to an over-estimate of the ratio, $\sum_i d_i^2 / \sum_i a_i^2$, and thus to an overestimate of \bar{d} , if repulsion phase linkage predominates, or if bias of V_d due to the linkage effect is greater than the bias of V_a due to linkage effects. In the advancement of the populations from the F2 to later generations by random mating, the amount of linkage disequilibrium will be expected to be reduced in each generation. Therefore, the estimates of V_m , V_{mp} , and \bar{d} from design III progenies with later generations which descended from F2 population by random mating should have less biases due to linkage disequilibrium. The estimates of V_{mp} in the advanced generations are expected to be smaller than the estimates in F2 generation regardless of linkage phase. The estimates of V_m in the advanced generations will be greater than the estimate in the F2 if repulsion linkage phase predominates, and smaller than in the F2 if coupling linkage predominates. If the coupling and repulsion linkage are of equal importance, the estimates of V_m in the later generations will be no different from the estimate in the F2 generation. Therefore, comparisons of the estimates of V_m , V_{mp} , and \bar{d} obtained after random mating F2 populations with the estimates obtained from F2 generation can provide information for the relative importance

of linkage disequilibrium in the F2 populations.

Significance of differences between variance components estimated from F2 and F2 Syn5 generations was tested by F-tests computed as ratio of appropriate mean squares. Tests of the hypothesis that $d > 1$ if allele frequency is 0.5 and loci are in linkage equilibrium are the ratios of V_{mp} to V_m .

In this experiment, the F2 plants used to produce design III progenies were also self-pollinated to produce the S1 lines in each population. Therefore, both S1 lines and design III progenies will estimate the genetic parameters for each population. If epistasis is absent, the expected components of genetic variance for the variance components of the expected mean squares for S1 lines (V_{s1}) and design III progenies are:

$$V_{s1} = V_a + V_d/4,$$

$$V_m = V_a/4,$$

$$V_{mp} = V_d.$$

We have three equations and two unknowns. V_a and V_d can be estimated by the least squares method from the three equations. The significance test of the model was conducted in the usual way for multiple regression analysis.

RESULTS

The means of the three inbred lines, two single crosses, and their F2 and F3 progenies are presented in Table 2. The yield of B84 was 3.1 q/ha greater than the yield of Mo17. The yield of B73 X Mo17, however, was about 50% greater than that of B73 X B84. The mean yields of F2 and F3 progenies from B73 X Mo17 were 38.8% and 18.8% greater than the mean yield of F2 and F3 progenies from B73 X B84, respectively. Progenies derived from B73 X Mo17 also had longer ears and earlier silk dates than progenies from B73 X B84. In F1 and F2 generations, B73 X Mo17 had greater ear diameter and more kernel rows than B73 X B84. In the F3 generation, the mean of progenies from B73 X Mo17 was equal to B73 X B84 for ear diameter, and less than B73 X B84 for kernel-row number. The ear height was slightly greater in B73 X Mo17 than in B73 X B84 for all generations.

The means of the six traits for the backcross progenies and S1 lines derived from F2 and F2 Syn5 generations of the two hybrids are listed in Table 3. For all traits, there were no significant differences between the means of backcrosses and S1 progenies derived from F2 generation and the means of backcrosses and S1 progenies derived from F2 Syn5 generation in B73 X Mo17. The mean yields of both backcross progenies and S1 lines derived from B73 X B84 were slightly increased from F2 to F2 Syn5 generation. The mean yields of backcross progenies derived from B73 X Mo17 were greater than from B73 X B84 in both F2 and F2 Syn5 generations. There were no significant differences between the mean yield of S1 lines derived from B73 X Mo17 and the mean yield of S1

Table 2. Progeny means of six traits for the two crosses in set four averaged over replications and environments

Cross	Progeny	Trait		
		Yield (q/h)	Ear height (cm)	Ear length (cm)
B73X Mo17	B73	34.4 \pm 2.1	97.9 \pm 5.7	12.3 \pm 0.22
	Mo17	41.4 \pm 3.4	86.7 \pm 4.7	13.5 \pm 0.33
	F1	108.7 \pm 2.2	108.4 \pm 6.9	20.8 \pm 0.30
	F2	90.1 \pm 4.8	109.9 \pm 2.3	17.3 \pm 0.62
	F3	57.6 \pm 1.6	90.3 \pm 1.6	16.0 \pm 0.21
B73X B84	B73	34.3 \pm 2.1	97.9 \pm 5.7	12.3 \pm 0.66
	B84	44.5 \pm 2.7	83.0 \pm 4.0	17.4 \pm 0.22
	F1	72.1 \pm 5.0	103.3 \pm 3.5	18.2 \pm 0.56
	F2	64.9 \pm 4.3	101.0 \pm 3.5	15.1 \pm 0.70
	F3	48.5 \pm 1.3	89.3 \pm 1.3	14.3 \pm 0.03

^a Days after July 1.

Trait		
Ear diameter (cm)	Silk date ^a	Kernel- row number
4.3 ± 0.05	24.3 ± 0.75	19.7 ± 0.33
4.1 ± 0.13	26.0 ± 0.02	14.2 ± 0.40
4.9 ± 0.03	18.5 ± 0.65	15.3 ± 0.19
4.9 ± 0.04	21.3 ± 1.25	17.6 ± 0.33
4.4 ± 0.03	21.0 ± 0.27	14.6 ± 0.22
4.3 ± 0.05	24.3 ± 0.75	17.9 ± 0.33
3.6 ± 0.07	23.8 ± 0.75	11.1 ± 0.24
4.4 ± 0.07	21.0 ± 0.41	14.7 ± 0.21
4.5 ± 0.05	22.5 ± 0.65	16.9 ± 0.33
4.4 ± 0.03	23.2 ± 0.32	16.4 ± 0.15

Table 3. Progeny means of six traits for four populations averaged over replications, sets, and environments

Population	Progeny ^a	Trait					
		Yield (q/h)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)	Silk date ^b	Kernel row number
B73XMo17 F2	BC1	77.0	104.1	16.4	4.7	20.3	16.4
	BC2	75.1	96.6	19.2	4.3	20.3	13.3
	S1	54.0	87.3	16.0	4.3	20.9	14.5
B73XMo17 F2 Syn5	BC1	77.5	102.1	16.5	4.7	20.1	16.5
	BC2	77.2	97.5	19.2	4.3	19.8	13.5
	S1	55.0	86.7	16.3	4.3	20.3	14.7
B73XB84 F2	BC1	62.8	104.3	15.0	4.7	22.2	17.6
	BC2	64.8	103.6	15.8	4.6	22.9	16.2
	S1	52.6	92.8	14.6	4.6	22.8	16.5
B73XB84 F2 Syn5	BC1	68.0	102.0	15.1	4.7	21.7	17.7
	BC2	66.6	99.7	16.1	4.6	22.0	16.5
	S1	54.3	87.7	14.7	4.4	22.0	16.9

^aBC1 is the backcross to B73, BC2 is the backcross to either Mo17 or B84, and S1 is the progenies after one generation of selfing.

^bDays after July 1.

lines derived from B73 X B84 in both F2 and F2 Syn5 generations. Backcross progenies and S1 lines from B73 X Mo17 also had longer ears and earlier silk dates than the backcross progenies and S1 lines derived from B73 X B84 in both F2 and F2 Syn5 generations. There were no significant differences between the progeny means from B73 X Mo17 and the progeny means from B73 X B84 for ear height and ear diameter.

The estimates of heterosis and inbreeding depression for the six traits measured from B73 X Mo17 and B73 X B84 are given in Table 4. The parental means of B73 X Mo17 were smaller than the parental means of B73 X B84 for yield and ear length, and greater than the parental means of B73 X B84 for ear height, ear diameter, and kernel-row number, respectively. The heterosis effects (h) of B73 X Mo17 were 125.5% and 170.8% greater than that of B73 X B84 for yield and ear length, respectively. The h estimates of B73 X Mo17 also were greater than the h estimates of B73 X B84 for ear height, ear diameter, and silk date. The h estimate of B73 X Mo17, however, was smaller than the h estimate of B73 X B84 for kernel-row number. On the other hand, the estimates of inbreeding depression in B73 X Mo17 were greater than in B73 X B84 for all traits measured.

The estimates of additive genetic variance and additive X environmental interaction from design III analysis are presented in Table 5 for all traits in each population. In B73 X Mo17, there were no significant changes for the estimates of additive genetic variance from F2 to F2 Syn5 generation for yield, ear length, and ear diameter. Estimates of additive variance decreased from F2 to F2 Syn5 generation

Table 4. Estimates of heterosis (h) and inbreeding depression for six traits of B73 X Mol7 and B73 X B84

Cross	Trait	\bar{P}^a	F1	h (%)	Inbreeding depression		
					F2/F1 (%)	F3/F1 (%)	F3/F2 (%)
B73 X Mol7	Yield(q/ha)	37.9	108.7	187.2	82.9	53.0	63.9
	Ear height(cm)	92.3	108.4	17.4	101.4	83.3	82.1
	Ear length(cm)	12.9	20.8	61.2	83.2	76.9	92.5
	Ear diameter(cm)	4.2	4.9	16.7	100	89.8	89.8
	Silk date ^b	25.2	18.5	-27.8	115.1	113.5	98.6
	Kernel-row number	16.1	15.3	-4.7	115.0	95.4	83.0
B73X B84	Yield(q/ha)	39.4	72.1	83.0	90.0	67.3	74.7
	Ear height(cm)	90.5	103.3	14.2	97.8	86.4	88.4
	Ear length(cm)	14.9	18.2	22.6	83.0	78.6	94.7
	Ear diameter(cm)	4.0	4.4	11.4	102.3	100	102.3
	Silk date ^b	24.1	21.0	-12.5	107.1	110.5	103.1
	Kernel-row number	14.5	14.7	1.4	115.0	111.6	97.0

^a \bar{P} is the parental means.

^bDays after July 1.

Table 5. Estimates of additive genetic variance the six traits from design III analysis pooled over sets and combined over environments

Cross	Trait	F2		F2 Syn5	
		Va ^a	Vae	Va	Vae
B73X Mol7	Yield(q/ha)	104.30±30.84	17.10±9.00	108.03±32.64	17.60±9.20
	Ear height(cm)	85.08±22.92	2.93±4.55	127.08±33.08	0.33±4.18
	Ear length(cm)	1.15±0.34	0.14±0.10	1.15±0.35	0.13±0.10
	Ear diameter -2 (cm)X10	3.41±0.88	-0.11±0.15	2.52±0.72	-0.09±0.16
	Silk date ^b	2.62±0.58	0.74±0.36	1.94±0.38	-0.33±0.33
	Kernel row number	2.08±0.34	-0.01±0.03	0.60±0.14	0.20±0.18
B73X B84	Yield(q/ha)	32.88±11.56	-7.73±5.30	55.38±17.92	2.53±6.83
	Ear height(cm)	55.08±15.88	1.20±4.30	45.83±14.60	8.07±5.32
	Ear length(cm)	0.62±0.21	0.09±0.09	0.81±0.26	0.11±0.10
	Ear diameter -2 (cm)X10	0.71±0.36	0.53±0.25	1.50±0.44	-0.21±0.14
	Silk date ^b	0.60±0.46	2.66±1.33	1.25±0.28	-0.31±0.38
	Kernel-row number	1.06±0.20	0.11±0.15	0.91±0.17	0.01±0.11

^a Va and Vae are the estimates of additive variance and interaction of additive X environment, respectively.

^b Days after July 1.

for silk date and kernel-row number, and increased for ear height. In B73 X B84, however, estimates of additive variance significantly increased from F2 to F2 Syn5 generation for silk date and ear diameter. There was no significant change for the estimates of additive variance from F2 to F2 Syn5 generation for yield, ear height, ear length and kernel-row number in B73 X B84. These results indicated that linkage disequilibrium had a different effect on the estimates of additive genetic variance in the populations derived from the two hybrids.

In general, estimates of additive variance from B73 X Mol7 were greater than from B73 X B84 for all traits except kernel-row number. For yield, the estimates of additive variance for B73 X Mol7 were about two to three times greater than the estimates for B73 X B84 in both F2 and F2 Syn5 generations, respectively. The estimates of additive genetic variance of kernel-row number for B73 X Mol7 was greater than for B73 X B84 in the F2 generation, and smaller than for B73 X B84 in the F2 Syn5 generation.

Significant estimates of additive X environment interaction for yield were observed in both F2 and F2 Syn5 generations for B73 X Mol7. Interaction of additive X environment estimates for yield were nonsignificant in B73 X B84 F2 and F2 Syn5 generations. Estimates of additive X environment interactions generally were relatively smaller than the estimates of additive genetic variance for all traits measured. This may be due to the similar environments for the three experiments conducted.

Estimates of dominance genetic variance and dominance X environment interaction are presented in Table 6. Estimates of dominance variance for yield significantly decreased from F2 to F2 Syn5 generation for both B73 X Mo17 and B73 X B84. Dominance variance estimates also decreased from F2 to F2 Syn5 generation for ear diameter in B73 X Mo17. There were no significant differences between the estimates of dominance variance from F2 and from F2 Syn5 generations for ear height, ear length, kernel-row number, and silk date in both B73 X Mo17 and B73 X B84. In B73 X B84, the dominance variance estimates were not significantly different from zero for kernel-row number in F2 generation and for ear height in both F2 and F2 Syn5 generations.

Dominance variance estimate for yield in B73 X Mo17 F2 Syn5 generation (48.84) was nearly five times greater than the estimate in B73 X B84 F2 Syn5 generation (10.73). Estimates of dominance variance for ear height, ear length, and ear diameter in B73 X Mo17 F2 and F2 Syn5 generations also were greater than the estimates in B73 X B84 F2 and F2 Syn5 generations.

The estimates of dominance X environment interaction were relatively small for all traits. In most instances, interaction of dominance X environment was not significant. This could be due to the similar environments for the experiments conducted.

The estimates of average level of dominance (\bar{d}) are listed in Table 7. Estimates of \bar{d} generally decreased from F2 to F2 Syn5 generations in both B73 X Mo17 and B73 X B84. Estimate of \bar{d} for yield decreased from 1.28 in F2 to 0.95 in F2 Syn5 generation in B73 X Mo17 and from 1.53 to

Table 6. Estimates of dominance genetic variance and dominance X environment interaction for six traits from design III analysis pooled over sets and combined over environments

Cross	Trait	F2		F2Syn5	
		Vd ^a	Vde	Vd	Vde
B73X Mo17	Yield(q/ha)	84.96±22.98	13.90±5.20	48.84±14.17	2.30±3.99
	Ear height(cm)	12.91±4.32	-2.60±2.02	14.71±4.70	-4.40±1.87
	Ear length(cm)	0.38±0.13	0.14±0.11	0.35±0.12	0.06±0.05
	Ear diameter -2 (cm)X10	1.02±0.30	-0.03±0.09	0.65±0.21	-0.12±0.08
	Silk date ^b	0.47±0.13	0.01±0.12	0.30±0.07	-0.45±0.05
	Kernel-row number	0.08±0.03	0.03±0.03	0.08±0.04	0.08±0.04
B73X B84	Yield(q/ha)	38.29±10.82	-4.65±3.11	10.73±5.19	1.65±3.81
	Ear height(cm)	1.91±3.01	9.00±3.33	3.23±2.56	1.25±2.45
	Ear length(cm)	0.19±0.07	-0.06±0.04	0.13±0.06	-0.06±0.04
	Ear diameter -2 (cm)X10	0.40±0.19	0.39±0.14	0.31±0.11	-0.31±0.06
	Silk date ^b	0.18±0.15	0.60±0.21	0.33±0.09	-0.23±0.08
	Kernel row number	0.08±0.03	0.07±0.04	0.03±0.02	-0.03±0.02

^a V_d and V_{de} are the estimates of dominance variance and interaction of dominance X environment, respectively;

^b Days after July 1.

Table 7. Estimates of average level of dominance (\bar{d}) for six traits from design III analysis pooled over sets and combined over environments for two crosses

Cross	Trait	F2	F2 Syn5
B73X Mo17	Yield(q/ha)	1.28	0.95
	Ear height(cm)	0.55	0.48
	Ear length(cm)	0.81	0.78
	Ear diameter(cm)	0.78	0.72
	Silk date ^a	0.60	0.56
	Kernel-row number	0.28	0.53
B73X B84	Yield(q/ha)	1.53	0.62
	Ear height(cm)	0.26	0.38
	Ear length(cm)	0.78	0.57
	Ear diameter(cm)	1.06	0.64
	Silk date ^a	0.77	0.73
	Kernel-row number	0.38	0.27

^a Days after July 1.

0.62 in B73 X B84. Estimates of d suggest that the average level of dominance was in partial to complete dominance range for all traits studied. The overdominance for yield observed in F2 was due to the bias of linkage disequilibrium. These results were similar to those reported by Gardner and Lonnquist (1959) and Moll et al. (1964).

Estimates of variance components from S1 lines analysis combined over environments are presented in Table 8. The magnitudes of S1 variance components in each population were similar to the estimates of additive genetic variance for the design III progenies. In B73 X Mol7, there were no significant changes for the S1 variance components from F2 S1 to F2 Syn5 S1 for yield, ear length, and silk date. S1 variance component in B73 X Mol7 increased for ear height, and decreased for ear diameter and kernel-row number in F2 Syn5 S1. The direction of change in S1 variance component from F2 S1 to F2 Syn5 S1 was consistent with that of additive variance in design III progenies.

In B73 X B84, there were small differences between the S1 variance component estimated from F2 S1 and F2 Syn5 S1 lines for ear length, ear diameter, silk date, and kernel-row number. The S1 variance component significantly decreased from F2 S1 to F2 Syn5 S1 for yield. The greater reduction of S1 variance component for yield in F2 Syn5 S1 may be partially due to the nonsignificant S1 X environment interaction in F2 S1 lines, and, thus, the S1 variance component was overestimated in F2 S1.

The variance component among B73 X Mol7 S1 lines was generally greater than among B73 X B84 S1 lines in both F2 S1 and F2 Syn5 S1 for all traits (Table 8). The variance component for yield among S1 lines

Table 8. Estimates of variance components and standard errors among S1 lines and S1 X environment interaction for each population combined over environments

Cross	Trait	F2		F2 Syn5	
		Vs1 ^a	Vs1.e	Vs1	Vs1.e
B73X Mo17	Yield(q/ha)	136.38±36.30	38.30±10.70	133.82±35.30	21.60±8.00
	Ear height (cm)	68.71±17.66	4.25±4.17	99.34±25.42	5.15±4.49
	Ear length (cm)	1.70±0.44	0.21±0.10	1.33±0.35	0.10±0.09
	Ear diameter ⁻² (cm)X10	4.48±1.12	0.30±0.20	1.23±0.38	0.37±0.19
	Silk date ^b	1.75±0.36	0.40±0.33	2.05±0.49	0.95±0.46
	Kernel-row number	1.83±0.31	0.15±0.08	0.56±0.10	0.08±0.04
B73X B84	Yield(q/ha)	65.93±17.33	2.90±4.90	32.32±11.07	19.20±7.50
	Ear height (cm)	60.88±15.57	0.60±3.60	47.34±12.25	-2.20±3.19
	Ear length (cm)	1.19±0.31	0.11±0.09	0.93±0.25	0.05±0.11
	Ear diameter ⁻² (cm)X10	1.16±0.34	0.04±0.16	1.18±0.33	-0.11±0.14
	Silk date ^b	1.05±0.21	-0.36±0.16	1.18±0.23	-0.41±0.16
	Kernel-row number	0.66±0.12	0.05±0.06	0.82±0.14	-0.02±0.05

^a Vs1 and Vs1.e are the estimates of variance among S1 lines and S1 X environment interaction, respectively.

^b Days after July 1.

derived from B73 X Mol7 was two and four times greater than the variance component among S1 lines derived from B73 X B84 in F2 S1 and F2 Syn5 S1, respectively.

The S1 X environment interaction for yield in B73 X Mol7 F2 S1 was greater than in B73 X B84 F2 S1. In F2 Syn5 S1, the estimate of S1 X environment interaction in B73 X Mol7 was similar to the estimate in B73 X B84. S1 X environment interaction estimates for the other traits were relatively small.

Estimates of genetic variance components and average levels of dominance from S1 and design III progenies combined analysis are listed in Table 9. The coefficients of determination (R^2) for the model that included additive and dominance components were greater than 0.90 for all traits except for ear diameter in B73 X Mol7 F2 Syn5 generation ($R^2 = 0.43$) and for yield in B73 X B84 F2 Syn5 generation ($R^2 = 0.86$). The failure of the model that included the additive and dominance components for ear diameter in B73 X Mol7 F2 Syn5 generation may be due to the relative small genetic variance and large sampling error.

The estimates of additive genetic variance obtained from S1 and design III combined analysis were consistent with the estimates from design III analysis for all traits except for yield in B73 X B84 F2 Syn5 generation. In B73 X B84, the estimate of additive genetic variance for yield decreased in F2 Syn5 generation from S1 and design III combined analysis. The estimate of additive genetic variance, however, increased in F2 Syn5 generation from design III analysis. The difference between the additive genetic variance estimates from S1 and design III combined

Table 9. Estimates of genetic variance components from S1 and design III combined analysis pooled over sets and combined over environments for two crosses

Cross	Trait	F2			F2 Syn5		
		Va ^a	Vd	\bar{d}	Va	Vd	\bar{d}
B73X Mol7	Yield(q/ha)	114.48	85.16	1.22	120.75	49.00	0.90
	Ear height(cm)	66.70	12.61	0.61	97.59	14.23	0.54
	Ear length(cm)	1.58	0.39	0.70	1.24	0.35	0.75
	Ear diameter (cm)	0.0417	0.0103	0.70	0.0116	0.0063	1.04
	Silk date ^b	1.69	0.46	0.74	1.97	0.30	0.55
	Kernel-row number	1.83	0.08	0.30	0.54	0.08	0.54
B73X B84	Yield(q/ha)	54.86	38.64	1.19	31.22	10.33	0.86
	Ear height(cm)	60.07	1.99	0.26	46.46	3.21	0.37
	Ear length(cm)	1.11	0.20	0.60	0.89	0.13	0.54
	Ear diameter (cm)	0.0064	0.0040	0.88	0.0113	0.0030	0.73
	Silk date ^b	0.98	0.19	0.62	1.11	0.33	0.77
	Kernel-row number	0.66	0.07	0.95	0.82	0.03	0.27

^aVa, Vd, and \bar{d} are the estimates of additive variance, dominance variance, and average level of dominance, respectively.

^bDays after July 1.

analysis and from design III analysis may be caused by the sampling error and the bias of additive X environment interaction. Because of the nonsignificant interaction of S1 X environment in F2 S1 lines and F2 Syn5 design III progenies, the estimates of additive variance for yield from F2 S1 lines and F2 Syn5 design III progenies may be overestimated in B73 X B84. The S1 and design III combined analysis would provide a better estimate.

The estimates of dominance variance from S1 and design III combined analysis were consistent with the estimates from design III analysis for all traits in both B73 X Mol7 and B73 X B84. The estimates of average level of dominance from S1 and design III analysis also were similar to the estimates from design III analysis. In both hybrids, estimates of \bar{d} were in partial to complete dominance range for all traits measured.

DISCUSSION

Hallauer and Miranda (1981) summarized the estimates of genetic variance components and other parameters for maize. The average estimates of additive and dominance variance of yield for F2 populations developed from a cross of two inbred lines were 585.1 ± 338.5 and 451.0 ± 593.0 (g/plant), respectively. Hallauer (1970) reported that the estimates of additive and dominance variance were 157 ± 30 and 174 ± 38 (g/plant) for BSSS maize population. In this study, the estimates of additive and dominance variance for B73 X Mo17 F2 population were 104.30 ± 30.84 and 84.96 ± 22.98 (q/ha), which are similar to the previous reports for F2 populations (Table 5 and 6). Estimates of additive and dominance variance for B73 X B84 F2 population were 32.88 ± 11.56 and 38.29 ± 10.82 (q/ha), respectively, which were smaller than the estimates from B73 X Mo17 F2 (Table 5 and 6). The estimates of additive and dominance variance for B73 X B84 F2, however, were only slightly smaller than the estimates for BSSS population reported by Hallauer (1970).

If there are a total of m loci controlling a trait and the gene effects for each locus are equal, then $V_a = \frac{1}{2}(ma)^2$ and $V_d = \frac{1}{4}(md)^2$, where "a" is additive allele effect, "d" is dominance effect of the two alleles at one locus, and "m" is the number of loci controlling a quantitative trait that is segregating. The greater additive and dominance variance in a population are caused by either a large number of segregating loci or greater "a" and "d" values at the segregating loci, or both. In our experiment, B73 is the common parent for B73 X Mo17 and B73

X B84; therefore, at least one allele is in common for each locus in B73 X Mol7 and B73 X B84. The yield of B84 was greater than that of Mol7 (Table 2). This indicated that the favorable loci controlling yield in B84 may be greater than, or at least equal to, the favorable loci number in Mol7. Therefore, the total favorable alleles in B73 X B84 would be no less than in B73 X Mol7. The great additive and dominance variance for B73 X Mol7 implies that there is a larger number of loci segregating for genes controlling yield. On the other hand, the relative smaller estimates of additive and dominance variance for B73 X B84 indicated that there was a relatively smaller number of loci segregating. This implies that some of favorable loci in B84 are the same as in B73, whereas the favorable alleles fixed in Mol7 are located at different loci with those in B73. The fact that the mean yield of S1 lines from B73 X Mol7 was equal to the mean yield of S1 lines from B73 X B84 also support this interpretation.

Since B73 and B84 were derived from BSSS and Mol7 includes Lancaster germplasm, this result suggests that inbred lines derived from the same population may have a certain number of loci fixed with common alleles. The greater differences for favorable alleles in B73 and Mol7 could be due to the different favorable allele frequencies at different loci within the BSSS population and within the Lancaster population; i.e., for some loci, favorable allele frequencies are higher in BSSS, and for other loci, the favorable allele frequencies are higher in Lancaster.

In both B73 X Mol7 and B73 X B84, the additive and dominance

variance accounted for most of the genetic variance for all traits. This suggests that the additive and dominance effects were the most important genetic effects in both high performance and related line hybrids. Epistatic effects do not to be important factors affecting these traits for both hybrids.

Significant reduction of dominance variance for yield estimated from F2 to F2 Syn5 generation indicated that linkage disequilibrium existed in both B73 X Mol7 and B73 X B84. Nonsignificant differences between estimates of additive variance for yield from F2 and from F2 Syn5 generation in B73 X Mol7 suggested that coupling and repulsion linkage effect may approximately cancel each other in these populations. In B73 X Mol7, the estimates of additive variance suggested that coupling phase linkage predominated for ear length, ear diameter, and kernel-row number, and that repulsion phase linkage predominated for ear height in the F2 generation. In B73 X B84, however, there were no significant differences between the estimates of additive variance from F2 and from F2 Syn5 generations for ear length, ear diameter, silk date, and kernel-row number. Coupling linkage phase was suggested for ear height in B73 X B84. Estimates of additive variance for yield from design III progenies were greater in the F2 Syn5 generation. Estimate of additive variance for yield decreased from the F2 to the F2 Syn5 generation for S1 and design III combined analysis for B73 X B84. The conflicting results obtained from design III progenies and from S1 and design III combined analysis for the estimates of additive variance in B73 X B84 may be partially due to the relative small proportion of

additive variance in the variance component among males and the greater sampling errors in design III progenies. On the other hand, the nonsignificance of male X environment interaction for both F2 and F2 Syn5 generations and of S1 X environment interaction among F2 S1 lines would contribute to an overestimate of additive variance in design III and an overestimate of S1 variance component among F2 S1 lines. Therefore, S1 and design III combined analysis provided a better estimate of additive variance.

The biases of genetic variance estimates due to linkage disequilibrium were less in B73 X B84 than in B73 X Mo17 for all traits. This suggested that linkage disequilibrium was of less importance for the population produced from inbred lines derived from same population, which was considered in linkage equilibrium. The linkage disequilibrium for yield observed in B73 X B84 may be due to the change of favorable allele frequencies in the improved BSSS populations.

Estimates of average level of dominance were in partial to complete dominance range for all traits. These estimates agreed with the previous reports by Gardner and Lonnquist (1959) and Moll et al. (1964). There was little difference between the estimates of average level of dominance in the populations developed from related and unrelated hybrids. The differences of average level of dominance estimated from B73 X Mo17 and from B73 X B84 for some traits may be due to linkage disequilibrium and predominant linkage phase in the two populations.

Estimates of average level of dominance, \bar{d} , were less than 1 in F2 Syn5 generation for both hybrids. These results were similar to the

previous reports for other maize populations (Gardner and Lonnquist, 1959, and Moll et al., 1964). It seems that overdominance was not important for controlling maize yield. However, $\bar{d} < 1$ cannot exclude the role of overdominance in controlling maize yield at some loci.

Suppose three loci control one trait, each locus with two alleles, and the level of dominance for the three loci is additive ($d = 0$), complete dominance ($d = 1$), and pure overdominance ($a = 0$), respectively. The average level of dominance estimated for these three loci would be complete dominance ($\bar{d} = 1$). Overdominance, however, does exist and plays an important role in the hybrid performance. The other argument concerning the absence of overdominance is the hybrid performance. If many loci control yield and the favorable alleles are completely dominant to the unfavorable alleles at each locus, the performance of the hybrid produced by two homozygous inbred lines depends on the number of favorable loci in each inbred line and the number of loci in which two inbred lines are fixed with different alleles. If the favorable alleles fixed in the two inbred lines are completely different from each other, the genotypic value of hybrid produced by the two inbred lines will be equal to the sum of the two inbred lines. Otherwise, the hybrid value should be smaller than the sum of the two parental inbred lines.

Therefore, if the level of dominance for each locus controlling yield is in partial to complete dominance, the hybrid yield could not be significantly greater than the total yield of the two parental inbred lines. Consider the yield of hybrids and their respective parental lines. The B73 X B84 F1 (72.1 q/ha) was less than the sum of B73 and B84

(78.8 q/ha). In B73 X Mol7, however, the F1 yield (108.7 q/ha) was greater than the sum of B73 and Mol7 (75.8 q/ha). Apparently, overdominance or other gene action should exist in B73 X Mol7. Therefore, the level of dominance for genes controlling maize yield may involve a complex gene action system, and different pairs of alleles may differ in the levels of dominance.

If the level of dominance is equal for all of the loci controlling a quantitative trait, \bar{d} would be overestimated if the linkage disequilibrium exists. However, if the levels of dominance for the loci controlling one trait are different, \bar{d} could be overestimated with linkage disequilibrium; \bar{d} would be overestimated with repulsion phase linkage of the additive loci or underestimated with coupling phase linkage of the additive loci. In this study, the estimates of dominance variance in F2 Syn5 were not significantly different from the estimates in F2 for ear height, ear length, and kernel-row number in B73 X Mol7. The additive variance estimates, however, increased for ear height, and decreased for ear length and kernel-row number from F2 to F2 Syn5 populations for B73 X Mol7. This may indicate the linkage disequilibrium only existed for the additive loci for these traits.

Experiments have shown that inbred lines from BSSS population have good combining ability with inbred lines from Lancaster Sure Crop. Therefore, maize breeders in the U.S Corn Belt tend to divide the source materials into two groups; group A contains the inbred lines derived from Lancaster Sure Crop, and group B contains the inbred lines derived from BSSS population. Breeders generally select inbred lines

from F2 populations produced by the inbred lines derived from same population and produce the hybrid by crossing group A inbred lines to group B inbred lines. Present study showed that significant genetic variance existed among S1 lines derived from both F2 and F2 Syn5 generations in B73 X B84. This indicated that selection from the population produced by two related inbred lines would be effective. The heterosis effect for yield (83%) in B73 X B84 F1 and the significant genetic variance in the derived population implied that favorable alleles fixed in B84 were different with the alleles fixed in B73 at many loci. Therefore, it should be possible to select an inbred line that was superior to the two parental lines from the population produced by B73 X B84. The selected line would also have good combining ability with the lines derived from Lancaster population. It seems an efficient inbred-hybrid breeding method. However, since some of the homozygous favorable alleles are fixed at same loci for the related lines and the lack of favorable alleles at some loci in the source population, further improvement of the inbred lines selected from the related population would become more difficult.

The large variance component among S1 lines derived from B73 X Mo17 population indicated that selection could be more efficient in the unrelated line populations than in related line populations. However, since the information is not available for the combining ability of the derived lines, testing for the combining ability for the selected lines from unrelated population would be more difficult. On the other hand, the expected mean value of the inbred lines derived from unrelated line

populations may not be greater than that of the lines from related line population. To overcome the disadvantages of the above two procedures of inbred lines development, the use of convergent selection or backcross methods to improve the parental lines for the unrelated line population could be an efficient procedure for inbred lines improvement.

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SECTION II. ESTIMATES OF GENETIC EFFECTS FROM GENERATION MEANS
IN TWO MAIZE SINGLE CROSSES

ABSTRACT

Genetic parameters were estimated from generation mean analysis in two maize (Zea mays L.) hybrids, B73 X Mo17 and B73 X B84. Ten generations for each cross were analyzed by two methods: Method I included seven generations: P1, P2, F1, F2, F2 S1, F2 BC1, and F2 BC2; and Method II included six generations: P1, P2, F1, F2 Syn5 S1, F2 Syn5 BC1, and F2 Syn5 BC2. Parameters estimated were additive, dominance, and digenic epistatic effects.

Heterosis for yield and other traits was greater in B73 X Mo17 than in B73 X B84. Dominance was the most important effect controlling the heterosis for yield and other traits in both B73 X Mo17 and B73 X B84. Epistatic effects were not important for most traits in both single crosses. Significant epistatic effects were detected for ear length and silk dates in B73 X Mo17 and for ear length and kernel-row number in B73 X B84. The greater heterosis observed for yield and other traits in B73 X Mo17 than in B73 X B84 were due to the greater positive dominance effects and smaller negative dominance X dominance effects in B73 X Mo17.

Linkage had an important effect on the estimates of epistatic effects from Method I for ear height and yield for both hybrids. This suggested that both linkage and epistatic effects were present in the segregating generations for yield and ear height. There were few differences between the estimates of genetic effects from Method I and from Method II for the other traits.

INTRODUCTION

Generation mean analyses have been used to estimate the gene effects for maize (Zea mays L.) yield and other traits in several experiments. Gamble (1962a, b) estimated the genetic effects of maize yield and five other traits from generation mean analysis and concluded that dominance effects were very important in maize yield. Darrah and Hallauer (1972) estimated the genetic effects of maize yield from generation means in four types of maize inbred lines. They reported that dominance effects were larger and had greater frequency of significance than additive effects; the epistatic effects estimated from good and poor lines were similar. Moreno-Gonzalez and Dudley (1981) reported that genetic effects estimated from generation mean analysis were similar in the maize hybrids produced by related and unrelated inbred lines.

Differences in genetic variance components between the populations derived from B73 X Mo17 and from B73 X B84 have been reported (Han, 1987). The objectives of this study were to estimate the genetic effects in the two maize hybrids, B73 X Mo17 and B73 X B84, and to make comparisons with the parameters estimated from the generation means for the two hybrids.

MATERIALS AND METHODS

Three inbred lines (B73, B84, and Mo17) were used as parents to make two F1 single crosses (B73 X Mo17 and B73 X B84). Both B73 and B84 were derived from 'Iowa Stiff Stalk Synthetic' (BSSS) (Hallauer et al., 1983). B73 and B84, therefore, are related lines. Mo17 was derived by pedigree selection from the cross of 187-2 X C103. Mo17's phenotypic appearance and performance in crosses are similar to C103, which was derived from 'Lancaster Sure Crop'. B73 X Mo17 was one of the best commercial hybrids in the U.S. Corn Belt. For each cross, the F2 generation was produced by selfing the F1 plants. F2 Synthetic 5 (F2 Syn5) population was obtained by random mating 250 F2 plants for five generations. Forty unselected plants from each F2 and F2 Syn5 generation for both crosses were used as male plants to produce backcross progenies. Each male plant was backcrossed to the two parental lines to produce BC1 and BC2 progenies. The F2 plants also were self-pollinated to produce S1 progenies. Each F2 plant, therefore, was used to produce the backcross progenies to their respective parents and self-pollinated.

All materials were evaluated in three environments. Details of the field arrangement and data collection were given in section I. Since inbred lines, F1, and F2 generations were only included in set 4, as described in section I, S1 and BC progenies only grown in set 4 were used to conduct generation mean analysis.

Data were analyzed by two methods: Method I included the two

parents, F1, F2, F2 S1 (F3), F2 BC1, and F2 BC2 generations, and Method II included the two parents, F1, F2, F2 Syn5 S1, F2 Syn5 BC1, and F2 Syn5 BC2 generations.

Two models proposed by Mather and Jinks (1982) were used in each method. Model I included additive and dominance gene effects, whereas Model II included additive, dominance, and digenic nonallelic interaction effects. Gamble's notation was used for convenience. The expected generation means for the two models for Method I are as follows:

Model I:

$$P1 = m + a$$

$$P2 = m - a$$

$$F1 = m + d$$

$$F2 = m + 1/2 d$$

$$F2 S1 = m + 1/4 d$$

$$F2 BC1 = m + 1/2 a + 1/2 d$$

$$F2 Bc2 = m - 1/2 a + 1/2 d$$

Model II:

$$P1 = m + a + aa$$

$$P2 = m - a + aa$$

$$F1 = m + d + dd$$

$$F2 = m + 1/2 d + 1/4 dd$$

$$F2 S1 = m + 1/4 d + 1/16 dd$$

$$F2 BC1 = m + 1/2 a + 1/2 d + 1/4 aa + 1/4 dd + 1/4 ad$$

$$F2 BC2 = m - 1/2 a + 1/2 d + 1/4 aa + 1/4 dd - 1/4 ad$$

P1 and P2 are the inbred parents, F2 S1, F2 BC1, and F2 BC2 are the self (S1) and backcross (BC1 and BC2) progenies derived from F2 generation. F1 and F2 are as defined before. "m" is the mean of all inbred lines derived from a P1 X P2 cross; "a" is the additive effect; "d" is the dominance effect; "aa" is the additive X additive effect; "dd" is the dominance X dominance effect; and "ad" is the additive X dominance effect.

In Mather and Jinks' (1982) model, the estimates of genetic parameters were based on the assumption of no linkage. If linkage is absent and the expected genetic drift is zero, the expected generation means for F2 Syn5 S1, F2 Syn5 BC1, and F2 Syn5 BC2 are equal to F2 S1, F2 BC1, and F2 BC2, respectively. Therefore, the models used in Method II were the same as in Method I except the F2 generation was absent. Linkage will not effect P1, P2, and F1 generations, and the linkage effects will be reduced by random mating in the F2 populations. The biases of the estimates of genetic effects from Method II would be smaller than those from Method I. Therefore, the differences between the genetic effects estimated from Method I and from Method II could be caused by linkage effects.

The parameters in the two models were estimated by the least squares analysis. Because of the unequal variances of mean squares for each generation, the means for each generation were weighted by the reciprocals of the squared standard errors of each mean. The standard errors associated with the estimated parameters were computed in the

usual way for multiple regression analysis. Predicted values were computed for each model.

RESULTS AND DISCUSSION

Performances of The Two Crosses

Generation means for each cross are presented in Table 1. The yield of B84 was 3.1 q/ha greater than that of Mol7. The yield of B73 X Mol7, however, was about 50% greater than that of B73 X B84. The mean yield of the B73 X Mol7 F2 was 38.8% greater than the mean yield of B73 X B84 F2. S1 progenies from B73 X Mol7 F2 also averaged 18.8% greater yield than the B73 X B84 F2 S1 progenies. Progenies derived from B73 X Mol7 also had longer ears and earlier silk date than the progenies from B73 X B84. The mean yield of backcross progenies derived from B73 X Mol7 was also greater than that from B73 X B84 in both F2 and F2 Syn5 generations. The mean yield of F2 S1 lines was slightly greater in B73 X Mol7 than in B73 X B84. The mean yield of F2 Syn5 S1, however, was slightly lower in B73 X Mol7 than in B73 X B84. Backcross and S1 progenies derived from B73 X Mol7 also had longer ears and earlier silk date than the backcross and S1 lines derived from B73 X B84.

The estimates of heterosis effects for yield and other traits also are included in Table 1. The parental mean of B73 X Mol7 was smaller than B73 X B84 for yield and ear length. The heterosis effects of B73 X Mol7, however, were 125.5% and 170.8% greater than that of B73 X B84 for yield and ear length, respectively. Heterosis effects were also greater in B73 X Mol7 than in B73 X B84 for ear height, ear diameter, and silk date. Heterosis was smaller in B73 X Mol7 than in B73 X B84 for kernel-row number.

Table 1. Progeny means of six traits for the two crosses in averaged over replications and environments

Cross	Progeny	Yield (q/h)	Ear height (cm)	Ear length (cm)
	B73	34.4 \pm 2.1	97.9 \pm 5.7	12.3 \pm 0.22
	Mo17	41.4 \pm 3.4	86.7 \pm 4.7	13.5 \pm 0.33
B73 X Mo17	F1	108.7 \pm 2.2	108.4 \pm 6.9	20.8 \pm 0.30
	F2	90.1 \pm 4.8	109.9 \pm 2.3	17.3 \pm 0.62
	F2 S1	57.6 \pm 1.6	90.3 \pm 1.6	16.0 \pm 0.21
	F2 BC1	75.8 \pm 1.5	103.3 \pm 1.7	16.3 \pm 0.15
	F2 BC2	77.7 \pm 1.7	97.5 \pm 1.7	19.2 \pm 0.16
	Syn5 S1	50.5 \pm 2.0	86.4 \pm 1.9	15.8 \pm 0.22
	Syn5 BC1	74.1 \pm 1.8	99.4 \pm 1.9	16.2 \pm 0.20
	Syn5 BC2	76.1 \pm 1.9	97.3 \pm 1.8	18.9 \pm 0.18
	h (%) ^b	187.2	17.4	61.2

^a Days after July 1.

^b h refers to heterosis, it was computed as $h = (F1 - P)/P$, where P is the parental mean.

Ear diameter (cm)	Silk date ^a	Kernel row number
4.3 \pm 0.05	24.3 \pm 0.75	19.7 \pm 0.33
4.1 \pm 0.13	26.0 \pm 0.02	14.2 \pm 0.40
4.9 \pm 0.03	18.5 \pm 0.65	15.3 \pm 0.19
4.9 \pm 0.04	21.3 \pm 1.25	17.6 \pm 0.33
4.4 \pm 0.03	21.0 \pm 0.27	14.6 \pm 0.22
4.7 \pm 0.02	20.6 \pm 0.29	16.5 \pm 0.16
4.3 \pm 0.03	20.6 \pm 0.26	13.3 \pm 0.12
4.3 \pm 0.03	20.7 \pm 0.40	15.4 \pm 0.11
4.7 \pm 0.03	20.4 \pm 0.27	16.7 \pm 0.15
4.3 \pm 0.02	19.7 \pm 0.22	13.7 \pm 0.10
16.7	-27.8	-0.8

Table 1. Progeny means of six traits for the two crosses in averaged over replications and environments

Gross	Progeny	Yield (q/h)	Ear height (cm)	Ear length (cm)
	B73	34.4 \pm 2.1	97.9 \pm 5.7	12.3 \pm 0.22
	Mo17	41.4 \pm 3.4	86.7 \pm 4.7	13.5 \pm 0.33
B73 X Mo17	F1	108.7 \pm 2.2	108.4 \pm 6.9	20.8 \pm 0.30
	F2	90.1 \pm 4.8	109.9 \pm 2.3	17.3 \pm 0.62
	F2 S1	57.6 \pm 1.6	90.3 \pm 1.6	16.0 \pm 0.21
	F2 BC1	75.8 \pm 1.5	103.3 \pm 1.7	16.3 \pm 0.15
	F2 BC2	77.7 \pm 1.7	97.5 \pm 1.7	19.2 \pm 0.16
	Syn5 S1	50.5 \pm 2.0	86.4 \pm 1.9	15.8 \pm 0.22
	Syn5 BC1	74.1 \pm 1.8	99.4 \pm 1.9	16.2 \pm 0.20
	Syn5 BC2	76.1 \pm 1.9	97.3 \pm 1.8	18.9 \pm 0.18
	h (%) ^b	187.2	17.4	61.2

^a Days after July 1.

^b h refers to heterosis, it was computed as $h = (F1 - P)/P$, where P is the parental mean.

Ear diameter (cm)	Silk date ^a	Kernel row number
4.3 \pm 0.05	24.3 \pm 0.75	19.7 \pm 0.33
3.6 \pm 0.07	23.8 \pm 0.75	11.1 \pm 0.24
4.4 \pm 0.07	21.0 \pm 0.41	14.7 \pm 0.21
4.5 \pm 0.05	22.5 \pm 0.65	16.9 \pm 0.33
4.4 \pm 0.03	23.2 \pm 0.32	16.4 \pm 0.15
4.6 \pm 0.02	23.1 \pm 0.62	17.5 \pm 0.12
4.5 \pm 0.02	23.1 \pm 0.28	16.1 \pm 0.14
4.5 \pm 0.02	22.6 \pm 0.32	16.7 \pm 0.13
4.7 \pm 0.02	22.6 \pm 0.31	17.4 \pm 0.11
4.5 \pm 0.02	22.5 \pm 0.31	16.2 \pm 0.13
11.4	-12.5	0.2

Estimates of Genetic Effects

Estimates of genetic effects from model I and model II for Method I are listed in Tables 2 and 3, respectively. In model II, significant epistatic effects were observed for ear length in both crosses, for silk date in B73 X Mol7, and for kernel-row number in B73 X B84. Epistatic effects were not significant for yield, ear height, and ear diameter in both crosses. Estimates of "aa" and "ad" generally were relatively small and either positive or negative. There were no apparent differences between the estimates obtained from B73 X Mol7 and from B73 X B84. Estimates of "dd" were negative in B73 X B84 for all traits except ear height. Estimates of "dd" were positive for ear height, silk date, and kernel-row number, and negative for yield, ear length, and ear diameter in B73 X Mol7. All negative estimates of "dd" were smaller in B73 X Mol7 than in B73 X B84.

In model I, significant dominance effects were observed for all traits except kernel-row number in both B73 X Mol7 and B73 X B84. In general, dominance effects estimated in B73 X Mol7 were greater than in B73 X B84. Dominance effect estimates of yield, ear length, and silk date, which showed greater heterosis in B73 X Mol7 than in B73 X B84, were also greater in B73 X Mol7 than in B73 X B84. Estimates of "m" were significant for all traits. The estimates of "m" from B73 X Mol7 were similar to those from B73 X B84 for all traits measured.

Additive effect estimates were relatively small compared to the dominance effects and "m" values in both crosses. These results are in good agreement with those of Gamble (1962a, b), Darrah and Hallauer (1972),

Table 2. Estimates of genetic effects of six traits from Method I model I over environments for two crosses

Cross	Trait	Genetic effect ^a		
		m	a	d
B73 X Mo17	Yield(q/ha)	39.69**	3.06	72.45**
	Ear height (cm)	80.33**	-5.76	42.08**
	Ear length (cm)	14.20**	2.36**	6.98**
	Ear diameter(cm)	4.18**	-0.32*	0.73*
	Silk date ^b	24.29**	1.51	-8.19*
	Kernel-row number	14.67**	-3.18**	0.54
B73 X B84	Yield(q/ha)	36.97**	2.79	48.42**
	Ear height(cm)	79.35**	-0.28	43.80**
	Ear length(cm)	13.30**	0.96**	3.94**
	Ear diameter(cm)	4.23**	-0.11	0.64*
	Silk date ^b	24.07**	0.70	-2.86**
	Kernel-row number	16.32**	-2.10	0.26

^am, a, and d are the estimates of mean and additive, and dominance effects, respectively.

^bDays after July 1.

*, **Indicate significant at 0.05 and 0.01 probability levels, respectively.

Table 3. Estimates of genetic effects of six traits from Method I model II over environments for two crosses

Cross	Trait	Genetic effects ^a					
		m	a	d	aa	ad	dd
B73 X Mol7	Yield(q/ha)	36.84	3.43	87.14**	0.85	-3.01	-15.24
	Ear height(cm)	83.46	0.13	21.76	-6.74	-12.11	33.68
	Ear length(cm)	13.69**	0.60	9.91*	-0.79	4.60*	-2.80*
	Ear diameter(cm)	4.03	-0.99	1.81	-0.77	1.22	-0.94
	Silk date ^b	22.36**	0.86	-5.97	2.78*	-1.72	2.11
	Kernel-row number	15.11	-1.99	-1.49	0.57	-2.50	1.69
B73 X B84	Yield(q/ha)	33.60	5.08	66.56	5.76	-5.71	-27.56
	Ear height(cm)	75.54	-6.91	64.20	14.02	14.04	-36.31
	Ear length(cm)	14.08**	2.55**	-0.22	0.77	-3.30*	4.33*
	Ear diameter(cm)	4.05	-0.34	1.76	-0.08	0.48	-1.42
	Silk date ^b	23.19	-0.25	0.74	0.91	0.67	-2.93
	Kernel-row number	14.85**	-3.40**	8.30**	-.36*	4.00**	-8.45**

^a m, a, d, aa, ad, and dd are the estimates of mean and additive, dominance, additive X additive, additive X dominance, and dominance X dominance effects, respectively.

^b Days after July 1.

*, ** Indicate significant at 0.05 and 0.01 probability levels, respectively.

and Moreno-Gonzalez and Dudley (1981). Estimates of additive effects for each cross were computed from the differences between the two parental lines. Mather and Jinks (1982) showed that

$$2rdS[d] = 2 \sum_k [d],$$

where rd is a measure of the gene distribution between the two parental lines ($rd = 1$, if all favorable genes in one parent, and $rd = 0$, if favorable genes are equally shared), $S[d]$ is the summed additive effects of k genes under consideration, k is the number of genes different in the two parents and $[d]$ is additive effect estimate under Mather and Jinks' notation. Therefore, the magnitude of additive effect not only depends on the gene effect for each individual locus, but also on the difference between genes fixed in the two inbred lines and the distribution in the two parents. If all favorable alleles were fixed in one line and unfavorable alleles fixed in another line ($rd = 1$), then the estimate of additive effect would be the summed effects of those genes under consideration. If, on the other hand, the favorable alleles are equally shared between the two parents ($rd=0$), the estimates of additive effect would be zero, no matter what the additive effects are for individual loci. In most cases, some favorable alleles are included in one parent, and others in another parent ($0 < rd < 1$). If $rd < 1$, then the additive effects estimated from generation mean analysis will be underestimated. Therefore, the small additive effects estimated from generation mean analysis does not imply that additive effects are not important in controlling the trait studied. The same reasoning is also true for the estimates of "aa" effects.

The correlation coefficients between the observed and predicted values from the parameters estimated in the two models by Method I are listed in Table 4. The high correlation between the observed and predicted values for model I indicated that additive and dominance effects were important in controlling the traits studied. The correlation coefficients estimated from B73 X Mo17 generally were greater than from B73 X B84 for model I. In B73 X B84, correlation coefficients between observed and predicted values from model II were higher than from model I for all traits studied. This indicated that the fit of model II was better than model I for B73 X B84. In B73 X Mo17, however, the correlation coefficients between observed and predicted values from model II were lower than those from model I for most traits measured.

Genetic Effects And Heterosis

If heterosis is defined as the difference between the F1 and the mean of two parents, the expected value of heterosis would be:

heterosis = d , for model I; and

heterosis = $d + dd - aa$, for model II.

In B73 X Mo17, the observed heterosis and expected heterosis from model I showed satisfactory agreement for all traits measured except for ear height (Table 6). In B73 X B84, however, observed heterosis was smaller than the expected heterosis from model I for all traits (Table 6). Good agreement of observed and predicted heterosis was obtained in model II for all traits in B73 X B84.

In both B73 X Mo17 and B73 X B84, dominance was the most important

Table 4. Correlation coefficients(r) between observed and predicted values for the six traits from Method I

Cross	Trait	r	
		Model I	Model II
B73 X Mol7	Yield(q/ha)	0.97	0.98
	Ear height (cm)	0.83	0.73
	Ear length (cm)	0.92	1.00
	Ear diameter(cm)	0.83	0.76
	^a Silk date	0.92	0.98
	Kernel-row number	0.77	0.79
B73 X B84	Yield(q/ha)	0.95	0.99
	Ear height(cm)	0.72	0.99
	Ear length(cm)	0.79	1.00
	Ear diameter(cm)	0.71	1.00
	^a Silk date	0.82	0.99
	Kernel-row number	0.84	1.00

^aDays after July 1.

Table 5. Observed and predicted heterosis effect for the six traits of B73 X Mo17 and B73 X B84

Cross	Trait	\bar{h}^a	h(I)	h(II)
B73 X Mo17	Yield(q/ha)	70.80	72.45	71.05
	Ear height(cm)	16.10	42.08	48.70
	Ear length(cm)	7.90	6.98	7.90
	Ear diameter(cm)	0.70	0.73	1.64
	Silk date ^b	-6.70	-8.19	-6.64
	Kernel-row number	-0.80	0.54	-0.37
B73 X B84	Yield(q/ha)	32.70	48.42	33.24
	Ear height(cm)	12.80	43.80	13.87
	Ear length(cm)	3.30	3.94	3.34
	Ear diameter(cm)	0.40	0.64	0.42
	Silk date ^b	-3.10	-2.86	-3.10
	Kernel-row number	0.20	0.26	0.21

^a \bar{h} is the observed heterosis, it was calculated by $\bar{h} = F_1 - P$, where P is the parental mean; h(I) and h(II) are the predicted heterosis from Model I and Model II, respectively; h(I) = d, and h(II) = d - aa + dd, where d, aa, and dd are dominance, additive X additive, and dominance X dominance effects, respectively.

^bDays after July 1.

effect that contributed to the heterosis of yield. In B73 X Mo17, estimates of dominance effects were greater than the estimates of epistatic effects for all traits except ear height. In B73 X B84, dominance effect estimates were smaller than the total epistatic effects for all traits except yield and ear height. These results may indicate that epistasis was more important in B73 X B84 than in B73 X Mo17. The greater heterosis observed in B73 X Mo17 than in B73 X B84 was due to the greater positive dominance effects and smaller negative dominance X dominance ("dd") effects for all traits.

Linkage Effects

Mather and Jinks (1982) discussed the effects of linkage on the estimates of genetic effects from generation mean analysis. If epistasis is present, linkage will bias all parameters from generation mean analysis in Mather and Jinks' model except additive effects. Since linkage will be broken by random mating, the linkage effects in F2 Syn5 S1, F2 Syn5 BC1, and F2 Syn5 BC2 would be smaller than in F2 S1, F2 BC1, and F2 BC2, respectively. P1, P2, and F1 will not be biased by linkage, therefore, the bias of estimates of genetic effects due to linkage in Method II would be smaller than in Method I. Assume genetic drift is small and negligible, the difference between the genetic effects estimated from Method I and from Method II could be caused by linkage disequilibrium in Method I.

Differences between the genetic parameters estimated from Method I and Method II were observed for yield, ear height, and kernel-row number

Table 6. Estimates of genetic effects of six traits from Method II model I over environments for two crosses

Cross	Trait	Genetic effect ^a		
		m	a	d
B73 X Mol7	Yield(q/ha)	35.97**	1.92	74.80**
	Ear height(cm)	74.77**	-1.89	46.40
	Ear length(cm)	13.90**	1.89	7.35*
	Ear diameter(cm)	4.07**	-0.37	0.84
	Silk date ^b	25.97**	-0.09	-12.05*
	Kernel-row number	15.42**	-3.71	0.24
B73 X B84	Yield(q/ha)	42.24**	0.20	47.67*
	Ear height(cm)	76.65**	-3.28	43.91
	Ear length(cm)	13.36**	1.10	3.97
	Ear diameter(cm)	4.3**	-0.19	0.47
	Silk date ^b	23.45**	-0.12	-2.13
	Kernel-row number	16.59**	-1.78	-0.08

^am, a, and d are the estimates of mean, additive, and dominance effect, respectively.

^bDays after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table 7. Estimates of genetic effects of six traits from
Method II model II over environments for two crosses

Cross	Trait	Genetic effect ^a					
		m	a	d	aa	ad	dd
B73 X Mol7	Yield(q/ha)	26.42	3.55	101.02	11.43	-3.10	-18.73
	Ear height (cm)	74.12	-5.60	44.46	18.18	7.00	-10.18
	Ear length (cm)	13.61	0.60	9.28	-0.71	4.20	-2.09
	Ear diameter(cm)	4.13	-0.10	0.63	0.07	0.60	0.13
	Silk date ^b	22.56	0.86	-8.57	2.59	-3.10	4.51
	Kernel-row number	15.19	-1.85	-1.06	0.86	-4.30	0.96
B73 X B84	Yield(q/ha)	38.82	5.10	76.26	0.58	-14.00	-42.98
	Ear height(cm)	74.31	-7.45	54.84	16.14	8.10	-25.84
	Ear length(cm)	13.95	2.55	0.45	0.90	-2.90	3.80
	Ear diameter(cm)	4.16	-0.35	1.73	-0.21	0.30	-1.49
	Silk date ^b	22.79	-0.25	-0.44	1.26	0.30	-1.36
	Kernel-row number	15.39	-3.40	7.22	-0.89	4.40	-7.91

^am, a, d, aa, ad, and dd are the estimates of mean and additive, dominance, additive X additive, additive X dominance, and dominance X dominance effects, respectively.

^bDays after July 1.

in B73 X Mol7 and for yield and ear height in B73 X B84. These results indicate that both epistasis and linkage were present in the recent segregating generations. Good agreement between the estimates of genetic effects from Method I and from Method II was observed for ear length, ear diameter, and silk date in B73 X Mol7 and for ear length, ear diameter, silk date, and kernel-row number in B73 X B84. These results suggest that epistasis and (or) linkage was absent for these traits. The results from random mating design III analysis (Han, 1987) also showed that linkage effects were not important in the estimates of genetic variance in the F2 generation for ear length and silk date in B73 X Mol7 and for ear length, ear diameter, silk date, and kernel-row number in B73 X B84. Present study seems to be in satisfactory agreement with the design III analysis.

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GENERAL CONCLUSIONS

The primary interest of this study was to compare the estimates of genetic variances, average levels of dominance, and genetic effects for two maize populations that descended from a high performance single cross, B73 X Mo17, and a related line single cross, B73 X B84. Heterosis for yield and other traits was greater in B73 X Mo17 than in B73 X B84.

In design III and combined design III and S1 progeny analysis, estimates of genetic variances for the B73 X Mo17 populations were greater than for the B73 X B84 populations for yield and other traits. Estimates of additive genetic variance for yield from B73 X Mo17 F2 and F2 Syn5 populations were about two and three times greater than those from B73 X B84 F2 and F2 Syn5 populations, respectively. Estimates of dominance genetic variance for yield from the B73 X Mo17 populations also were much greater than those from the B73 X B84 populations. These results suggested that there were more heterozygous loci in B73 X Mo17 than in B73 X B84 for genes controlling yield and other traits.

Estimates of average levels of dominance were in partial to complete dominance range in both populations for all traits. These results do not exclude the existence of overdominance for some loci. However, the levels of dominance for majority of genes controlling maize yield should be in the partial to complete dominance range. There was little difference between the estimates of average level of dominance from B73 X Mo17 and from B73 X B84. This suggested that the levels of dominance

were similar for genes in good performance hybrid and in the related line hybrid.

Estimates of dominance variance and average levels of dominance for yield decreased from F2 populations to F2 Syn5 populations for both hybrids. This suggested that linkage disequilibrium was present in the F2 populations. Estimates of additive variance for yield from F2 populations were not significantly different with those from F2 Syn5 populations for both hybrids. Therefore, the effects of coupling and repulsion phase linkages may cancel each other in the F2 populations.

Results from Section II indicated that dominance was an important effect in the expression of heterosis for yield and other traits in both hybrids. Since the estimates of additive effects depend on the distribution of genes in the parental lines, the importance of additive effects in controlling yield and other traits couldn't be estimated from in these two crosses. Epistatic effects for yield and most other traits were not significant in both B73 X Mol7 and B73 X B84.

Dominance effects estimated for B73 X Mol7 were greater than for B73 X B84 for all traits. The greater heterosis observed for yield and other traits in B73 X Mol7 than in B73 X B84 was because of the larger positive dominance effects and smaller negative dominance X dominance effects in B73 X Mol7. Since the estimates of the average levels of dominance for B73 X Mol7 populations were similar to those from B73 X B84 populations, the greater dominance effects estimated in B73 X Mol7 were contributed to the greater number of heterozygous loci in B73 X Mol7.

Biases of the estimates of genetic effects due to linkage disequilibrium were not important for most of traits in both hybrids. This suggested that linkage and (or) epistasis were absent in the populations. Linkage biases of estimates of genetic effects were observed for yield and ear height in B73 X Mol7 and for yield in B73 X B84. These results indicated that both linkage and epistasis existed in the two hybrids for these traits.

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APPENDIX

Table A1. Analysis of variance, means, and coefficients of variation (c.v.'s) for the six traits pooled over four sets within environments and combined over environments

Sources of variation	Degrees of freedom	Mean squares		
		Yield (q/ha)	Ear height (cm)	Ear length (cm)
Environments (E)	2	1476.2	52399.9**	110.7*
Sets(S)	3	1734.4	434.5	33.0
E X S	6	1791.9*	1239.2**	15.4**
Replications/SXE	12	522.4*	369.8*	3.4
Types (T)	1	196168.0**	103320.6**	1126.2**
E X T	2	1205.5**	804.0**	4.7
S X T	3	65.7	285.7	2.0
E X S X T	6	51.5	70.2	2.5
Error (a)	12	142.6**	119.5**	1.3*
Entries (G)/T/S	473	575.2**	308.6**	16.0**
Backcrosses (BC)	316	538.9**	227.6**	17.9**
S1 lines (S1)	157	648.2**	471.5**	12.2**
E X G/T/S	945	90.9**	47.8**	1.01**
E X BC	632	91.0**	48.7**	0.96**
E X S1	313	90.8**	46.0**	1.10**
Error (b)	1418	56.8	38.8	0.75
BC error	948	60.1	38.3	0.73
S1 error	470	50.1	39.8	0.81
Total	2883			
BC mean (c.v. %)		(10.9)	(6.1)	(5.1)
S1 mean (c.v. %)		(13.2)	(7.1)	(5.9)

^a Days after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Mean squares			
Ear diameter (cm)	Degrees of freedom	Kernel-row (no.)	Silk date ^a (no.)
0.0125	1	0.027	207.5
0.1824	3	4.679**	94.0
0.2255	3	0.620	125.2
0.1068*	8	0.164	43.2**
22.1487**	1	42.722**	62.9**
0.2028*	1	0.047	12.8*
0.0090	3	1.303	2.9
0.0518	3	0.588	2.2
0.0363**	8	0.744*	1.6
0.1997**	473	10.717**	9.8**
0.2020**	316	11.371**	8.7**
0.1950**	157	9.402**	12.0**
0.0190**	472	0.422**	2.2**
0.0172**	316	0.402**	2.1**
0.0224	156	0.462**	2.3**
0.0165	945	0.359	1.6
0.0159	632	0.330	1.43
0.0176	313	0.419	1.98
1921			
(2.8)		(3.6)	(5.7)
(3.0)		(4.1)	(6.5)

Table A2. Analysis of variance of yield, ear height, ear length, and ear diameter for backcross progenies pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares			
		Yield (g/ha)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)
Backcrosses(BC)/S	312	508.6**	227.3**	17.63**	0.2002**
(B73XMol7)F2					
(P1)BC /S	76	497.1**	299.0**	16.29**	0.3440**
(B73XMol7)Syn5					
(P2)BC /S	72	375.8**	292.2**	15.62**	0.2981**
(B73XB84)F2					
(P3)BC /S	76	220.8**	137.9**	3.25**	0.0673**
(B73XB84)Syn5					
(P4)BC /S	76	174.9**	128.1**	3.99**	0.0567**
P1BC vs P2BC /S	4	416.3*	315.9**	4.14*	0.1448**
P3BC vs P4BC /S	4	787.1**	678.6**	3.55*	0.1327**
P1&P2BC vs P3&P4BC /S	4	14739.6**	726.5	630.15**	1.0795**
Environments(E)					
X BC /S	624	90.2**	48.6*	0.95**	0.0173*
E X P1BC /S	152	87.5**	43.3	0.98**	0.0163
E X P2BC /S	144	77.1*	34.0	0.89*	0.0144
E X P3BC /S	152	58.3	47.2	0.75	0.0227**
E X P4BC /S	152	79.7**	46.5	0.80	0.0129
E X P1vsP2 BC /S	8	84.8	25.5	1.41	0.0073
E X P3vsP4 BC /S	8	75.3	54.9	0.97	0.0246
E X P1&P2vsP3&P4 BC /S	8	1202.9	499.1	7.82	0.0759
BC error	948	60.1	38.3	0.73	0.0159

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A3. Analysis of variance of silk date and kernel-row number for backcross progenies pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares	
		Silk date ^a	Kernel row number
Backcrosses (BC)/S	312	8.70**	11.45**
(B73XMo17)F2			
(P1)BC /S	76	5.16**	12.64**
(B73XMo17)Syn5			
(P2)BC /S	72	3.23**	10.90**
(B73XB84)F2			
(P3)BC /S	76	5.04**	3.70**
(B73XB84)Syn5			
(P4)BC /S	76	2.93**	2.73**
P1BC vs P2BC /S	4	6.31**	2.86**
P3BC vs P4BC /S	4	23.75**	3.07**
P1&P2BC vs P3&P4BC /S	4	331.73**	328.46**
Environments (E)			
X BC /S	312	2.10**	0.41*
E X P1BC /S	76	2.19*	0.34
E X P2BC /S	72	1.20	0.51**
E X P3BC /S	76	3.21**	0.44
E X P4BC /S	76	1.02	0.33
E X P1vsP2 BC /S	4	0.75	0.16
E X P3vsP4 BC /S	4	2.32	0.57
E X P1&P2vsP3&P4 BC /S	4	17.49**	0.63
BC error	632	1.43	0.33

^a Days after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A4. Analysis of variance of yield, ear height, ear length, and ear diameter from Design III analysis for (B73X Mo17) F2 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares			
		Yield (q/ha)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)
Parents(P) /S	4	478.5*	2002.1**	249.42**	4.7939**
Males(M) /S	36	398.6**	298.0**	4.39**	0.1166**
M X P /S	36	597.7**	110.5**	3.28**	0.0770**
E X P /S	8	100.8	141.6**	1.18	0.0422**
E X M /S	72	85.7**	42.7	0.94	0.0143
E X MXP /S	72	87.9**	33.1	1.00*	0.0153
BC error	948	60.1	38.3	.73	0.0159

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A5. Analysis of variance of yield, ear height, ear length, and ear diameter from Design III analysis for (B73X Mo17)F2Syn5 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares			
		Yield (q/ha)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)
Parents(P) /S	4	234.2	687.4**	218.61**	4.1520**
Males(M) /S	34	410.6**	420.0**	4.37**	0.0902**
M X P /S	34	357.7**	117.8**	2.97**	0.0526**
E X P /S	8	102.1	31.1	0.98	0.0200
E X M /S	68	86.5**	38.8	0.92	0.0146
E X MXP /S	68	64.7	29.6	0.85	0.0134
BC error	948	60.1	38.3	0.73	0.0159

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A6. Analysis of variance of yield, ear height, ear length, and ear diameter from Design III analysis for (B73X B84) F2 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares			
		Yield (q/ha)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)
Parents(P) /S	4	345.8	197.3*	21.41**	0.4438**
Males(M) /S	36	147.1**	205.4**	2.73**	0.0451*
M X P /S	36	280.5**	67.7	1.76**	0.0477**
E X P /S	8	212.7**	29.3	0.89	0.0568**
E X M /S	72	48.5	40.1	0.87	0.0238**
E X MXP /S	72	50.8	56.3**	0.62	0.0236**
BC error	948	60.1	38.3	0.73	0.0159

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A7. Analysis of variance of yield, ear height, ear length, and ear diameter from Design III analysis for (B73X B84)F2 Syn5 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares			
		Yield (q/ha)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)
Parents(P) /S	4	102.3	200.3	33.40**	0.3042*
Males(M) /S	36	230.0**	187.9**	3.32**	0.0577**
M X P /S	36	127.8**	60.2	1.39**	0.0282**
E X P /S	8	369.1**	62.9	1.54*	0.0438*
E X M /S	72	63.9	50.4*	0.90	0.0127
E X MXP /S	72	63.4	40.8	0.61	0.0097
BC error	948	60.1	38.3	0.73	0.0159

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A8. Analysis of variance of silk date and kernel-row number from Design III analysis for (B73XMol7)F2 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares	
		Silk date ^a	Kernel row number
Parents(P) /S	4	1.40	194.85**
Males(M) /S	36	7.41**	4.47**
M X P /S	36	3.33**	0.71*
E X P /S	4	9.02**	0.21
E X M /S	36	2.17**	0.32
E X MXP /S	36	1.45	0.38
BC error	632	1.43	0.33

^a Days after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A9. Analysis of variance of silk date and kernel row number from Design III analysis for (B73XMol7)F2Syn5 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares	
		Silk date ^a	Kernel row number
Parents(P) /S	4	2.66	174.56**
Males(M) /S	34	4.81**	1.73**
M X P /S	34	1.72**	0.81*
E X P /S	4	9.20**	0.68
E X M /S	34	0.93	0.53*
E X MXP /S	34	0.52	0.48*
BC error	632	1.43	0.33

^a Days after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A10. Analysis of variance of silk date and kernel row number from Design III analysis for (B73XB84)F2 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares	
		Silk date ^a	Kernel row number
Parents(P) /S	4	18.17**	40.04**
Males(M) /S	36	5.29	2.57**
M X P /S	36	3.33	0.79
E X P /S	4	0.54	0.16
E X M /S	36	4.09**	0.44*
E X MXP /S	36	2.62**	0.47**
BC error	632	1.43	0.33

^a Days after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A11. Analysis of variance of silk date and kernel row number from Design III analysis for (B73XB84) F2 Syn5 population pooled over sets and combined over environments

Source of variation	Degree of freedom	Mean squares	
		Silk date	Kernel row number
Parents(P) /S	4	2.58	28.82**
Males(M) /S	36	3.61**	2.15**
M X P /S	36	2.30**	0.41
E X P /S	4	0.45	0.32
E X M /S	36	1.12	0.34
E X MXP /S	36	0.98	0.27
BC error	632	1.43	0.33

^a Days after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A12. Analysis of variance of yield, ear height, ear length, and ear diameter for S1 lines pooled over sets within environments and combined over environments

Source of variation	Degree of freedom	Mean Squares			
		Yield (g/ha)	Ear height (cm)	Ear length (cm)	Ear diameter (cm)
S1/Set(S)	154	641.9**	475.9**	11.85**	0.1750**
(B73XMo17)					
F2(P1) S1/S	36	945.0**	460.5**	11.44**	0.2922**
(B73XMo17)					
Syn5(P2) S1/S	34	896.1**	646.1**	8.99**	0.0952**
(B73XB84)					
F2(P3) S1/S	36	451.5**	406.2**	8.13**	0.0877**
(B73XB84)					
Syn5(P4) S1/S	36	282.4**	319.4**	6.47**	0.0184
P1 vs P2 S1/S	4	1225.8**	211.3**	12.10*	0.3684**
P3 vs P4 S1/S	4	529.2**	944.5**	8.84*	0.3601**
P1&P2 vs P3&P4 S1/S	4	229.7	1000.7**	124.52**	0.9987**
Environments(E)					
X S1/S	308	92.1**	46.2**	1.11**	0.0448**
E X P1 S1 /S	72	126.7**	48.3	1.22**	0.0235
E X P2 S1 /S	68	93.2**	50.1	1.00*	0.0213
E X P3 S1 /S	72	55.9	41.0	1.02*	0.0184
E X P4 S1 /S	72	88.5**	35.4	0.90	0.0154
E X P1 vs P2 S1 /S	8	75.6	12.6	2.47**	0.0294
E X P3 vs P4 S1 /S	8	81.0	96.7**	1.94*	0.0158
E X P1&P2vsP3&P4 S1/S	8	157.5**	121.0**	1.45	0.1212**
S1 error	470	50.1	39.8	0.81	0.0176

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.

Table A13. Analysis of variance of silk date and kernel row number for S1 lines pooled over sets within environments and combined over environments

Source of variation	Degree of freedom	Mean Squares	
		Silk date ^a	Kernel row number
S1/Set(S)	154	11.85**	8.87**
(B73XMo17)			
F2(P1) S1/S	36	9.28**	8.04**
(B73XMo17)			
Syn5(P2) S1/S	34	12.07**	2.51**
(B73XB84)			
F2(P3) S1/S	36	5.44**	3.16**
(B73XB84)			
Syn5(P4) S1/S	36	5.87**	3.65**
P1 vs P2 S1/S	4	13.89**	9.77**
P3 vs P4 S1/S	4	13.14**	3.49**
P1&P2 vs P3&P4 S1/S	4	141.45**	99.03**
Environments(E)			
X S1/S	154	2.39**	0.46**
E X P1 S1	36	2.78*	0.72**
E X P2 S1	34	3.87**	0.27
E X P3 S1	36	1.26	0.51
E X P4 S1	36	1.17	0.38
E X P1 vs P2 S1	4	3.58**	0.44
E X P3 vs P4 S1	4	1.19	0.42
E X P1&P2vsP3&P4 S1	4	7.37**	0.21
S1 error	313	1.98	0.42

^aDays after July 1.

*, ** Indicate significance at 0.05 and 0.01 probability levels, respectively.