

71-14,217

DARRAH, Larry Lynn, 1943-

GENETIC PARAMETERS ESTIMATED FROM GENERATION  
MEANS IN FOUR DIALLEL SETS OF MAIZE INBREDS.

Iowa State University, Ph.D., 1970  
Agronomy

University Microfilms, A XEROX Company, Ann Arbor, Michigan

THIS DISSERTATION HAS BEEN MICROFILMED EXACTLY AS RECEIVED

GENETIC PARAMETERS ESTIMATED FROM GENERATION MEANS  
IN FOUR DIALLEL SETS OF MAIZE INBREDS

by

Larry Lynn Darrah

A Dissertation Submitted to the  
Graduate Faculty in Partial Fulfillment of  
The Requirements for the Degree of  
DOCTOR OF PHILOSOPHY

Major Subject: Plant Breeding

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University  
Of Science and Technology  
Ames, Iowa

1970

## TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	3
MATERIALS AND METHODS	31
EXPERIMENTAL RESULTS	45
DISCUSSION	136
SUMMARY	154
LITERATURE CITED	157
ACKNOWLEDGEMENTS	160
APPENDIX	161

## INTRODUCTION

Knowledge of the component processes of a complex synthetic system is essential to any attempt at modification of the final product. Plant breeders attempt to modify the gene structure of their crop species to produce a more desirable result. How the genes act and interact will determine the methods by which change should be attempted and the degree of success to be expected.

The characters dealt with in this process are generally quantitative in nature; that is, controlled by several genes, each having a small effect, and modified by the environmental forces. We wish to examine the genetic parameters which characterize the quantitative expression of gene action. Commonly, the characterization is based either on genotypic values or genotypic variances; the former method has been selected for this study.

Sprague (1955) expressed a need for such information in order to obtain "maximum efficiency of breeding techniques and resulting progress." Early models afforded estimates of effects due to single loci and their independent additive action. More recently interaction between loci, termed epistasis, has come of interest partially due to statements associating hybrid vigor with this nonallelic interaction [Hull (1945), Jinks and Jones (1958)]. Incorporation of this epistasis into prediction methods has been worked on by Eberhart, Russell, and Penny (1964) and others.

The purpose of this study is to estimate the genetic parameters for four Types of maize inbreds and to compare parameters to detect if the different Types show differing magnitudes of effects. In the process, non-epistatic and epistatic gene action will be examined to determine appropri-

ateness of the model used. A model suggested by Hayman (1958) and modified by Gamble (1962a) will be applied. Plant characters examined are: days to mid-silk, plant height, ear height, kernel row number, ear length, ear diameter, yield, and 300-kernel weight.

Twenty-two maize inbreds have been categorized into four Types with seven in each Type, some inbreds being multiply classified. Type I (1<sup>st</sup> Cycle) consisted of inbreds which were isolated directly from old open-pollinated varieties; Type II (2<sup>nd</sup> Cycle) inbreds were selected from planned crosses of inbreds, or synthetic varieties; Type III inbreds were "good" with respect to agronomic features; and Type IV inbreds were "poor". Comparisons are to be made between Types I and II to determine if the inbreds from different sources have similar effects. Types III and IV will be compared to determine if there is an association between good and poor inbreds and their genetic effects.

## REVIEW OF LITERATURE

## Concepts of Gene Action and Epistasis

The phenotypic measure of a quantitative character (P) may be expressed as the sum of independent contributions due to genotype (G), environment (E), and the interaction of genotype and environment (GE),

$$P = G + E + GE.$$

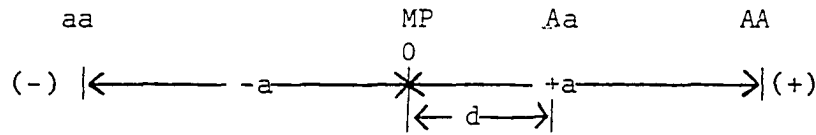
Likewise the phenotypic variance may be partitioned into genotypic variance ( $\sigma_G^2$ ), environmental variance ( $\sigma_E^2$ ), and interaction variance ( $\sigma_{GE}^2$ ),

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2.$$

The genotypic portion of the phenotypic variance was further divided by Fisher (1918) into an additive portion due to average effects of genes ( $\sigma_A^2$ ), a portion resulting from dominance effects ( $\sigma_D^2$ ), and a portion resulting from epistatic effects ( $\sigma_I^2$ ). The dominance effects were considered as being from allelic interactions, while the epistatic effects were from nonallelic interactions. He further showed the distribution of these genetic components of variance among various relatives in random mating populations. Fisher assumed that epistasis, while defined, was negligible.

The basic concept used by Fisher was three phases of a single Mendelian factor: AA, Aa, and aa, where AA is the positive homozygote and aa is the negative. No dominance relation is implied by the use of upper and lower case letters. Fisher took the deviation of AA from the midparent (MP) to be +a and the deviation of aa to be -a. The deviation of the

heterozygote (Aa) from the midparent was  $d$ .



In classical genetic terms if  $d = |a|$  then complete dominance was present, if  $d < |a|$  there was incomplete dominance, and if  $d = 0$  there was no dominance. The additive effect of the A gene was defined as "a", while the dominance effect due to the Aa genotype was defined as  $d$ .

Fisher, Immer, and Tedin (1932) changed terminology in considering the parental difference as  $2d$  as opposed to  $2a$  and termed the dominance effect  $h$  instead of  $d$ .

No further partitioning of genetic variance occurred until Cockerham (1954) divided the epistatic variance into four components. He defined additive x additive variance ( $\sigma_{AA}^2$ ) as arising from the interaction of the additive effect at one locus with that at another locus; additive x dominance variance ( $\sigma_{AD}^2$ ) from the interaction of the additive effect at one locus with the dominance effect at another; dominance x additive variance ( $\sigma_{DA}^2$ ) from the interaction of the dominance effect at the first locus with the additive effect of the second; and dominance x dominance variance ( $\sigma_{DD}^2$ ) from the interaction of the dominance effect at one locus with the dominance effect at another. Commonly  $\sigma_{AD}^2$  and  $\sigma_{DA}^2$  are not separated, but are collectively termed  $\sigma_{AD}^2$ . The notation was extended by Cockerham to three loci and a general form presented,

$$\sigma_I^2 = \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2.$$

Progress in working with means was largely limited to the scaling tests of Mather (1949) which only served to detect epistasis. Anderson and Kempthorne (1954) presented a generation mean analysis yielding terms due to: (a) the overall mean plus locus effects and interactions of the fixed loci; (b) the variable effects plus the interaction of these effects with fixed loci; and (c) the interactions of all possible pairs of variable loci plus the interaction of these interactions with the fixed loci. The genetic implications arising from this partition were obscure.

Hayman (1958) outlined a generation mean analysis based on the d and h terms of Fisher et al. (1932). The parameters were summed effects and deviations over all loci affecting a character and consisted of d for pooled additive effects, h for pooled dominance effects, i for pooled additive x additive effects, j for pooled additive x dominance effects, and l for pooled dominance x dominance effects. This was an exact parallel to the partition of variance by Cockerham (1954).

#### Methods of Estimating Types of Gene Action

Epistasis per se was detectable by the scaling tests of Mather (1949). Expectations of generation means were worked out and then generation means were combined in a linear contrast whose expectation was zero. The contrasts and their variances are shown below.

<u>Contrast</u>	<u>Contrast variance</u>
$A = 2\overline{BC}_1 - \bar{P}_1 - \bar{F}_1$	$V_A = 4V_{\overline{BC}_1} + V_{\bar{P}_1} + V_{\bar{F}_1}$
$B = 2\overline{BC}_2 - \bar{P}_2 - \bar{F}_1$	$V_B = 4V_{\overline{BC}_2} + V_{\bar{P}_2} + V_{\bar{F}_1}$
$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$	$V_C = 16V_{\bar{F}_2} + 4V_{\bar{F}_1} + V_{\bar{P}_1} + V_{\bar{P}_2}$



$\bar{P}_1$  and  $\bar{P}_2$  refer to the means of parent 1 and parent 2;  $\bar{F}_1$  is the mean of cross  $P_1 \times P_2$ ;  $\bar{F}_2$  is the mean of the  $F_1$  generation selfed; and  $\overline{BC}_1$  and  $\overline{BC}_2$  are the means of the backcrosses to  $P_1$  and  $P_2$ . The criteria of scaling were that (a) the genetic effects must on the average be additive, and (b) the contribution made by nonheritable agents must be independent of genotype. If scaling was adequate A, B, and C would equal zero within the limits of sampling error. Lack of fit would be due to epistasis. Similar contrasts over environments might be compared to detect genotype  $\times$  environment interaction.

Jinks (1956) used the same contrasts differently. The genetic expectations of the generations in the absence of epistasis were:

$$\begin{aligned}\bar{P}_1 &= M + \Sigma d, & \bar{F}_1 &= M + \Sigma h, & \overline{BC}_1 &= M + \frac{1}{2}\Sigma d + \frac{1}{2}\Sigma h, \\ \bar{P}_2 &= M - \Sigma d, & \bar{F}_2 &= M + \frac{1}{2}\Sigma h, \text{ and } & \overline{BC}_2 &= M - \frac{1}{2}\Sigma d + \frac{1}{2}\Sigma h.\end{aligned}$$

M is an overall mean,  $\Sigma d$  is the net additive effect, and  $\Sigma h$  the net dominance effect. The genetic expectations of A, B, and C were zero, thus, Jinks solved for  $\overline{BC}_1 = \frac{1}{2}(\bar{P}_1 + \bar{F}_1)$ ,  $\overline{BC}_2 = \frac{1}{2}(\bar{P}_2 + \bar{F}_1)$ , and  $\bar{F}_2 = \frac{1}{4}(2\bar{F}_1 + \bar{P}_1 + \bar{P}_2)$ . In the presence of epistasis these equations do not hold; hence, a  $\chi^2$  test with three degrees freedom was calculated with the quantities  $\overline{BC}_1$ ,  $\overline{BC}_2$ ,  $\bar{F}_2$  as the observed values and the linear combinations of the other generation means as the expected values. A significant  $\chi^2$  indicated presence of nonallelic interaction.

Kempthorne (1957) pointed out that scaling tests based on means retain the property of detecting epistasis regardless of linkage, though sensitivity may be lowered in the presence of linkage.

Evidence of nonallelic gene interaction in maize was obtained by

Bauman (1959) by comparing the average performance of two inbred (A and B) x tester (T) single-crosses with the performance of the tester x the single-cross of the two inbreds.

<u>Cross</u>	<u>Expectation based on any degree of dominance</u>	<u>epistasis</u>
A x T	$X_1$	$X_1$
B x T	$X_2$	$X_2$
(AxB) x T	$(X_1 + X_2)/2$	$(X_1 + X_2 + d)/2$

The "d" term above signified epistasis, but it was only a portion of the epistasis present and thus a qualitative demonstration.

A similar method was employed by Sprague et al. (1962) in comparing single versus three-way cross means. The method is illustrated below:

<u>Single cross</u>	<u>Three-way cross</u>	
1 x 2	(1 x 2) x 3	
1 x 3	(1 x 3) x 2	
<u>2 x 3</u>	<u>(2 x 3) x 1</u>	
$\bar{X}_1$	$\bar{X}_2$	$\bar{X}_1 - \bar{X}_2 = \text{epistasis.}$

The reasoning behind this comparison and that of Bauman was that in the single-crosses, for the two locus case, only three of nine possible genotypes could occur. In the three-way cross all nine genotypes could occur. On an allelic basis, all combinations occurred in both types of crosses, but six additional types of nonallelic combinations were available in the three-way cross and, to the extent that the two different loci were not independently additive in their effects, epistasis would be detected.

All of the previous models and(or) methods only detected presence or absence of epistasis; no quantification of any of the components of means or variances was made.

Anderson (1953) and Anderson and Kempthorne (1954) proposed a model for the study of quantitative inheritance based on an analogy to factorial experiments. They described features considered desirable in a model as: (a) additivity of parameters, (b) parameters having a genetic meaning, (c) applicability to a genotypic value for any number of loci, and (d) adaptability of the model with respect to increasing assumptions, i.e., that increasing assumptions resulted in dropping model terms.

Consideration was given to what Anderson and Kempthorne (1954) termed fixed loci such as AAbb which were alike in  $P_1$  and  $P_2$ , variable loci such as AaBb, and all types of interactions. The factorial analogy came in by denoting genotypes as follows:  $bb = b_0$ ,  $Aa = a_1$ ,  $AABb = a_2b_1$ . The effects were defined in terms of genotypes as  $A_0 = (a_0b_0 + 2a_0b_1 + a_0b_2)/4 - \mu$  where  $\mu$  was the overall mean. After defining  $A_i$  for  $i = 0, 1, 2$ , and likewise for  $B_j$ , in the two locus case, the genotypes were then expressed as effects, e.g.,  $a_ib_j = \mu + A_i + B_j + A_iB_j$ . Six orthogonal parameters were developed:

K = contribution due to the overall mean plus locus effects and interactions of the fixed loci;

E, F = contributions due to the variable effects plus the interaction of these effects with the fixed loci; and

G, L, M = contributions due to the interactions of all possible pairs of variable loci plus the interaction of the interactions with the fixed loci.

Genetically  $K_2$  is the  $F_2$  generation mean; E and F collectively are additive

and dominance effects; and G, L, and M are epistatic effects [Gamble (1962a)]. Within each of the above classes of effects, the parameters were confounded which made interpretation difficult.

The model assumed linkages and lethal genes were absent and constant viability for all genotypes. The generations used in this thesis are shown as defined by Anderson's and Kempthorne's parameters:

$$\begin{aligned}
 P_1 &= K_2 + F + M, \\
 P_2 &= K_2 - 2E - F + 4G + 2L + M, \\
 F_1 &= K_2 + E + G, \\
 F_2 &= K_2, \\
 F_3 &= K_2 - \frac{3}{4}E + \frac{9}{16}G, \\
 BC_1 &= K_2 + \frac{1}{2}E + \frac{1}{2}F + \frac{1}{4}G + \frac{1}{4}L + \frac{1}{4}M, \\
 BC_2 &= K_2 - \frac{1}{2}E - \frac{1}{2}F + \frac{1}{4}G + \frac{1}{4}L + \frac{1}{4}M, \\
 BC_1 \text{ self} &= K_2 + \frac{1}{2}F + \frac{1}{4}M, \text{ and} \\
 BC_2 \text{ self} &= K_2 - E - \frac{1}{2}F + G + \frac{1}{2}L + \frac{1}{4}M.
 \end{aligned}$$

Parameters, which lacked orthogonality but which were more readily interpretable, were described by Hayman and Mather (1955). In the digenic case they were:  $d_a$ , the additive effect of gene A;  $h_a$ , the dominance effect of gene A;  $d_b$ , the additive effect of gene B;  $h_b$ , the dominance effect of gene B;  $i_{ab}$ , the interaction of  $d_a$  with  $d_b$ ;  $j_{b|a}$ , the interaction of  $h_a$  with  $d_b$ ;  $j_{a|b}$ , the interaction of  $d_a$  with  $h_b$ ; and  $\ell_{|ab}$ , the interaction of  $h_a$  with  $h_b$ . They showed the 3 x 3 Punnett square for the digenic case with effects for each genotype. From the 9:3:3:1, the restrictions to obtain 12:3:1, 15:1, 13:3, 9:3:4, and 9:7 ratios were given. Application of these terms to scaling tests was discussed since  $E[\bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 - 4\bar{F}_2] = 0$

or if  $\neq 0$  then the expectation is  $2i_{ab} + \frac{1}{4}l_{ab}$  for 2 genes.

Hayman (1958) applied the parameters of Hayman and Mather (1955) to the generation mean structure. Subscripts were dropped leaving terms defined as follows:

$$d = \sum_a d_a \theta_a,$$

$$h = \sum_a h_a$$

$$i = \sum_{a \times b} i_{ab} \theta_a \theta_b,$$

$$j = \frac{1}{2} \sum_{a \times b} (j_{ab} \theta_a + j_{ba} \theta_b), \text{ and}$$

$$l = \sum_{a \times b} l_{ab}.$$

Summations were over all genes by which two parent inbred lines differed. The  $\theta$ 's indicated state of association in the parents; +1 when  $P_1$  contained the positive homozygote and -1 when  $P_2$  contained the positive homozygote. (Note that Hayman wrote  $P = P_1$  and  $P' = P_2$ ; however, for consistency with Gamble (1962a) subscripts will be used.) Hence,  $d$  measured pooled additive effects,  $h$  measured pooled dominance effects,  $i$  measured pooled additive x additive interactions,  $j$  measured pooled additive x dominance interactions, and  $l$  measured pooled dominance x dominance interactions.

In deriving the parameters to describe each generation, Hayman (1958) used the  $F_2$  as a background population. The process was to write out the generations in terms of one locus so genotypes and genotype frequencies were available for each. Then Hayman equated each generation to the midparent plus or minus the effects substituted for the genotypes; e.g.,  $\frac{1}{8}Aa$  was  $\frac{1}{8}h$ ,  $\frac{3}{8}AA$  was  $\frac{3}{8}d$ , and  $\frac{1}{4}aa$  was  $-\frac{1}{4}d$ , then these were summed over like terms. Next, Hayman changed to an  $F_2$  background by setting  $F_2 = MP + \frac{1}{2}h = m$  and subtracting  $m$  from each other generation. The epistatic parameter coefficients

were then entered according to the following equation:

$$\text{Generation}_x = m + \alpha_x d + \beta_x h + \alpha_x^2 i + 2\alpha_x \beta_x j + \beta_x^2 \ell.$$

The generations were expressed as below where BS<sub>1</sub> is BC<sub>1</sub> selfed:

$$\begin{aligned} P_1 &= m + d - \frac{1}{2}h + i - j + \frac{1}{4}\ell, \\ P_2 &= m - d - \frac{1}{2}h + i + j + \frac{1}{4}\ell, \\ F_1 &= m + \frac{1}{2}h + \frac{1}{4}\ell, \\ F_2 &= m, \\ F_3 &= m - \frac{1}{4}h + \frac{1}{16}\ell, \\ BC_1 &= m + \frac{1}{2}d + \frac{1}{4}i, \\ BC_2 &= m - \frac{1}{2}d + \frac{1}{4}i, \\ BS_1 &= m + \frac{1}{2}d - \frac{1}{4}h + \frac{1}{4}i - \frac{1}{4}j + \frac{1}{16}\ell, \text{ and} \\ BS_2 &= m - \frac{1}{2}d - \frac{1}{4}h + \frac{1}{4}i + \frac{1}{4}j + \frac{1}{16}\ell. \end{aligned}$$

The analysis proceeded by fitting the three parameter model by weighted least squares and testing as a  $\chi^2$  with six degrees of freedom. If there was a lack of fit, then the six parameter model was tested. Significant deviations, i.e., lack of fit to the six parameter model, were attributed to higher order epistasis or linkage.

Hayman (1958) stated that linkage affects only the epistatic terms in the generation means; however, Van der Veen (1959) and later Hayman (1960) corrected this statement. Van der Veen said, "Generation means lead to estimates of genetic parameters which are biased by linkage, except for those estimates of parameters or their linear functions which are already provided by parents and F<sub>1</sub>." Hayman (1960) gave these examples:

$$\hat{d} - \hat{j} = \frac{1}{2}(P_1 - P_2),$$

$$\hat{h} - \hat{i} = F_1 - \frac{1}{2}(P_1 - P_2), \text{ and}$$

$$\hat{m} + \frac{1}{2}\hat{h} + \frac{1}{4}\hat{\ell} = F_1.$$

Problems arose in the interpretation of additive and dominance effects in the presence of epistasis. Hayman stated, "it is not possible to obtain epistasis-free expectations of the generation means from  $m$ ,  $d$ , and  $h$  of the six-parameter model." The parameters obtained from fitting the three parameter model were used. The reasoning was that a given locus' additive effect in a given generation would be defined against a given set of other locus effects and their interactions. These would differ from generation to generation; hence, comparisons should not be made between effects measured against different backgrounds where there was interaction between the effect and its background.

Further information on the separation of epistatic from additive and dominance variation was provided by Hayman (1960). He grouped genetic systems into three types and discussed appropriate action for each. Group 1 was characterized as having no significant epistasis and significant additivity and(or) dominance. If the three parameter model fit, no problem existed in interpretation.

Group 2 showed significant epistasis but it was small when compared to additivity and(or) dominance. Group 2 was compared to agricultural trials where statistical differences were present, but they were of no economic importance. Estimators used in this case were those of group 1 after Hayman (1958). The modification was made on the standard deviations of the estimators where he suggests multiplying by  $(\chi^2 f)^{-\frac{1}{2}}$ , where  $f$  is the number

of degrees of freedom of the  $\chi^2$  indicating significant epistasis.

Group 3 exhibited significant epistasis, additivity, and(or) dominance where epistasis was of a similar magnitude to the other effects. This was the situation alluded to by Hayman (1958) where unique estimates of additivity and dominance were unavailable. Hayman (1960) looked to comparison of observed and expected means as the only choice. The importance of the three forms of epistasis might be assayed but not related to additivity or dominance.

Gamble (1962a, 1962b) reanalyzed his thesis data [Gamble (1957)] in accordance with Hayman's 1958 model. He reparameterized the model to follow the pattern established by workers with variances. Thus where A represented additive variance, a was the additive effect in the mean analysis. The correspondence between Gamble's parameters, Anderson and Kempthorne's (1954) and Hayman's (1958) were given by Gamble (1962a):

<u>Gene effect</u>	<u>Gamble</u>	<u>Anderson &amp; Kempthorne</u>	<u>Hayman</u>
Mean	m	$K_2$	m
Additive	a	$E + F$	d
Dominance	d	$2E$	h
Additive x additive	aa	$G + L + M$	i
Additive x dominance	ad	$2G + L$	j
Dominance x dominance	dd	$4G$	l

The expectations of the generation means need not be repeated here since there is a one to one relation in the reparameterization.

Gamble discussed the assumptions of Anderson and Kempthorne (1954)



which were [Gamble (1962a)]: (a) multiple alleles absent, (b) linkages absent, (c) lethal genes absent, (d) constant viability of all genotypes, and (e) environmental effects additive with the genotypic value. He stated no serious bias would occur due to (a), (c), or (d) since only the  $F_2$  and backcrosses were segregating. (Note: Gamble used six generations:  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$ , and  $BC_2$ .) Further, he permitted multiple alleles only if mutation occurred or the parental lines were not homozygous; the former being of low probability and the latter unlikely, since the lines used were maintained by selfing. Lethal genes were also unlikely due to maintenance of lines by selfing. Gamble (1962a) referenced Kempthorne (1957) regarding bias due to linkage. He stated, "when epistasis is present there is bias in aa and dd since linkage equilibrium is improbable in the early generations of a cross."

The most recent model for estimation of gene effects from genotypic values was the general model of Eberhart and Gardner (1966). Their model was applicable to pure lines, inbred lines with any degree of inbreeding, open pollinated varieties, and synthetic varieties subject to the restriction that they were in Hardy-Weinberg equilibrium. Multiple alleles and an arbitrary number of loci were allowable. The assumptions given were: diploid inheritance, equilibrium within each variety, and no epistasis other than additive x additive. Hence their model estimated additive, dominance, and additive x additive effects.

The following parameters were defined by Eberhart and Gardner (1966):

$\mu$  = an overall mean,

$a_k$  = additive effect for variety k,

$aa_k$  = additive x additive effect for variety k,

$d_k$  = a measure of inbreeding depression in variety k, and

$h_{kk'}$  = a measure of heterosis in the cross of varieties k and k'.

The expectations of generation means were as follows:

$$P_k = Y_k = \mu + a_k + aa_k + d_k,$$

$$F_1 = Y_{kk'} = \mu + \frac{1}{2}(a_k + aa_k + a_{k'} + aa_{k'} + d_k + d_{k'}) + h_{kk'} \\ + aa_{kk'},$$

$$F_2 = Y_{kk'}^{S1} = \mu + \frac{1}{2}(a_k + aa_k + a_{k'} + aa_{k'}) + \frac{1}{4}(d_k + d_{k'}) + \frac{1}{2}h_{kk'} \\ + aa_{kk'},$$

$$F_3 = Y_{kk'}^{S2} = \mu + \frac{1}{2}(a_k + aa_k + a_{k'} + aa_{k'}) + \frac{1}{8}(d_k + d_{k'}) + \frac{1}{4}h_{kk'} \\ + aa_{kk'},$$

$$BC_k = Y_{kk' \cdot k} = \mu + \frac{3}{4}(a_k + aa_k) + \frac{1}{4}(a_{k'} + aa_{k'}) + \frac{3}{4}d_k + \frac{1}{4}d_{k'} \\ + \frac{1}{2}h_{kk'} + \frac{3}{4}aa_{kk'}, \text{ and}$$

$$BS_k = Y_{kk' \cdot k}^{S1} = \mu + \frac{3}{4}(a_k + aa_k) + \frac{1}{4}(a_{k'} + aa_{k'}) + \frac{3}{8}d_k + \frac{1}{8}d_{k'} \\ + \frac{1}{4}h_{kk'} + \frac{3}{4}aa_{kk'}.$$

To obtain  $P_{k'}$ ,  $BC_{k'}$ , and  $BS_{k'}$ , the  $k'$  must be interchanged for  $k$  and the  $k$  for  $k'$  in all subscripts. Note the  $F_2$  and  $F_3$  differ from the  $F_1$  and  $F_2$  by a factor of  $\frac{1}{2}$  for the coefficients of  $d_k$  and  $h_{kk'}$  terms; likewise for the  $BC_k$  and  $BS_k$  generations. If inbred lines were used as parents, then  $d_k = 0$  in the  $P_k$  equation.

Eberhart and Gardner (1966) further partitioned  $h_{kk'}$  into average heterosis ( $\bar{h}$ ), variety heterosis ( $h_k, h_{k'}$ ), and specific heterosis ( $s_{kk'}$ )

where four or more varieties were used in a diallal:

$$h_{kk'} = \bar{h} + h_k + h_{k'} + s_{kk'}.$$

As with Hayman's 1958 model Eberhart and Gardner indicated confounding of  $a_k$  and  $aa_k$  if  $aa_k$  existed. They suggested estimating  $a_k^* = a_k + aa_k$  such that the mean of an inbred line was  $\mu + a_k^*$ . The other generations were similarly expressed and predictions could be made.

The relation between Eberhart and Gardner's (1966) parameters and those of Hayman (1958) assuming absence of additive x dominance and dominance x dominance effects was:

$$\begin{aligned} m &= \mu + \frac{1}{2}h_{12} + aa_{12}, \\ d &= a_1^* = a_1 + aa_1 = -a_2^* = -(a_2 + aa_2), \\ h &= h_{12}, \text{ and} \\ i &= -aa_{12}. \end{aligned}$$

All of the previous models and(or) methods are based on generation means; i.e., genotypic values versus genetic variances as used in the covariance of relatives and mating designs of Comstock and Robinson (1948).

Cockerham (1954) partitioned the epistatic variance into components as described previously. He also showed the distribution of these components in the covariances of relatives and presented the following formula:

$$\text{COV}(XY) = \sum_{\substack{n \\ A,D=0 \\ 1 < A+D < n}} p^A q^D \sigma_{AD}^2.$$

In this formulation  $\sigma_{20}^2 = \sigma_{AA}^2$ ,  $\sigma_{01}^2 = \sigma_D^2$ , etc. Where the relation is parent-offspring,  $p = \frac{1}{2}$  and  $q = 0$ . For half-sibs,  $p = \frac{1}{4}$  and  $q = 0$ , and for

full-sibs,  $p = \frac{1}{2}$  and  $q = \frac{1}{4}$ .  $p^A q^D$  is termed the correlation between epistatic deviations.

Chi (1965) applied genetic covariance theory to progenies resulting from two generations of controlled matings. He utilized the covariances of half-sibs, full-sibs, cousins, uncle-nephew, and no genetic covariance in estimating genetic components of variance.

Effects of linkage on the covariances of relatives was the subject of a paper by Cockerham (1956a). He stated that covariances of relatives, where one is an ancestor of the other, were not affected by linkages if one assumed a random mating population and no position effects. Further, covariances of relatives where one was not an ancestor of the other were affected by recombination frequencies less than  $\frac{1}{2}$ ; the lower the recombination the higher the covariance.

Schnell (1963) disagreed with Cockerham's (1956b) statement on the covariance of relatives where one is an ancestor of the other. Schnell concluded that the only case where linkage had no effect was that of parent-offspring, versus the more general statement by Cockerham (1956b).

The mating systems, commonly called Design I and Design II, were published by Comstock and Robinson (1948). At that time the designs were used to estimate  $\sigma_A^2$  and  $\sigma_D^2$  and assumed no epistasis. Presently, by combining Design I and II experiments on the same material, enough equations are available to estimate  $\sigma_{AA}^2$ ,  $\sigma_{AD}^2$ , and  $\sigma_{DD}^2$ . In 1948 they were primarily concerned with estimating the degree of dominance, "a":

$$"a" = (\bar{a}^2)^{1/2} = \left( \frac{2\sigma_D^2}{\sigma_A^2} \right)^{1/2}.$$

In the Design I experiment a single random male was mated to a number of females. The analysis contained sums of squares due to males, females within males, and error. Expected mean squares were manipulated to solve for the genetic components of variance according to the following relations:

$$\sigma_m^2 = \text{COV}(\text{HS}) = \frac{1}{4}\sigma_A^2 \text{ and}$$

$$\sigma_{f/m}^2 = \text{COV}(\text{FS}) - \text{COV}(\text{HS}) = \frac{1}{4}\sigma_A^2 + \frac{1}{4}\sigma_D^2.$$

Design II involved mating a series of males to a series of females giving sources of variation among males, among females, males x females, and error. The equations manipulated were:

$$\sigma_m^2 = \sigma_f^2 = \text{COV}(\text{HS}) = \frac{1}{4}\sigma_A^2 \text{ and}$$

$$\sigma_{mf}^2 = \text{COV}(\text{FS}) - 2\text{COV}(\text{HS}) = \frac{1}{4}\sigma_D^2.$$

Estimation of the epistatic components required the inbreeding coefficient (F) to be one in the Design II experiment, whereas, the inbreeding coefficient was zero in the equations above. When  $F = 1$ , the coefficients in the expectations for Design II were different, which permitted more parameters to be estimated. Use of half-sib and full-sib covariances at two levels of inbreeding was suggested by Cockerham (1956a). Assumptions of the analysis as presented by Cockerham (1956a) were: (a) diploid inheritance, (b) no position effects, (c) no maternal effects, and (d) no linkages. The general expressions

$$\text{COV}(\text{FS}) = \sum_{i,j} \left( \frac{1+F}{2} \right)^{i+2j} \sigma_{ij}^2 \text{ and } \text{COV}(\text{HS}) = \sum_i \left( \frac{1+F}{4} \right) \sigma_{io}^2$$

were given by Cockerham (1956a), where  $F$  was the inbreeding coefficient of the parents, and  $i$  and  $j$  were the number of times  $A$  and  $D$  occurred in the variance term. The genetic expectations were as follows, where subscripts 0 and 1 were used as indicating level of inbreeding for Design I and Design II, respectively:

$$\sigma_{m_0}^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 + \dots,$$

$$\sigma_{f/m_0}^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{4}\sigma_D^2 + \frac{3}{16}\sigma_{AA}^2 + \frac{1}{8}\sigma_{AD}^2 + \frac{1}{16}\sigma_{DD}^2 + \dots,$$

$$\sigma_{m_1}^2 = \sigma_{f_1}^2 = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 + \dots, \text{ and}$$

$$\sigma_{mf_1}^2 = \sigma_D^2 + \frac{1}{2}\sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2.$$

Robinson and Comstock (1955) used a third mating design in addition to the Design I and Design II described. Design III was constructed by the backcross matings of  $F_2$  plants to the two homozygous lines from which the  $F_2$  was derived. Components of the analysis of variance were  $F_2$  parents and  $F_2$  parents  $\times$  inbred lines. The equations relating the expected mean squares and genetic components were  $\sigma_m^2 = \frac{1}{4}\sigma_A^2$  and  $\sigma_{mL}^2 = \sigma_D^2$ , where  $m$  refers to the  $F_2$  male parent and  $L$  to the inbred lines. A quantity termed level

of dominance =  $\left\{ \frac{\sigma_D^2}{\sigma_A^2} \right\}$  was similar to the previous degree of dominance and was

used in interpreting the relative sizes of  $\sigma_A^2$  and  $\sigma_D^2$ . (Note: In this paper  $\sigma_d^2 = \sigma_D^2$  and  $\sigma_g^2 = \sigma_A^2$ , where the latter symbols are used for uniformity.)

Diallel cross designs constituted the last method of estimating gene action. Parents and reciprocal  $F_1$  crosses make up the possible entries in these designs. Diallel analysis permits estimation of forms of additive and dominance variation, general and specific effects, and some epistatic

variation. In this section,  $D$  is related to additive genetic variance and  $H$  to dominance variance. Jinks (1954) partitioned the second degree statistics into variances and covariances using the diallel. From these, he obtained estimates of additive and dominance variances and the degree of dominance. The following description of his method is given in his terminology. Define  $u_a$  = the proportion of parental lines AA,  $v_a = (1-u_a)$  = the proportion aa,  $+d_a$  as the effect of gene A, and the deviation of the heterozygote from the midparent =  $h_a$ . Then

$$\begin{aligned} D &= 4\sum uvd^2, & H_1 &= 4\sum uvh^2, \\ H_2 &= 16\sum u^2v^2h^2, \text{ and} & F &= 8\sum uv(u-v)dh. \end{aligned}$$

Note that if  $u = v = \frac{1}{2}$ ,  $D$  became  $\sum d^2$  and  $H_1 = H_2 = \sum h^2$  as would occur in the cross of two inbred lines.  $D$  and  $H_1$  related directly to additive and dominance variance, respectively, while  $H_2$  related to the ratio of positive to negative allelomorphs in the parental lines and  $F$  concerned the ratio of dominant to recessive allelomorphs.

Jinks (1954) gave the following compositions of variances and covariances:

$$\begin{aligned} \text{Variance of the parents} &= V_{OL0} = D, \\ \text{Mean variance of } F_1\text{'s in an array} &= V_{LL1} = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}F, \\ \text{Variance of } F_1\text{'s} &= V_{OL1} = \frac{1}{4}D + \frac{1}{4}H_1 - \frac{1}{4}H_2 - \frac{1}{4}F, \\ \text{Covariance of parent and offspring} &= W_{OL01} = \frac{1}{2}D - \frac{1}{4}F. \end{aligned}$$

In the diallel, an array referred to all progenies of a common parent, i.e., all  $F_1$ 's with a given inbred line as a parent. The estimate of degree of dominance was given as  $H_1/D$ .

Hayman (1954) listed the assumptions of the diallel cross as (a) diploid segregation, (b) no differences between reciprocal crosses, (c) no epistasis, (d) no multiple allelism, (e) homozygous parents, and (f) genes independently distributed between the parents. In this paper he reestablished the formulae of Jinks (1954) and described how to detect nonallelic gene interaction in addition to estimating additive and dominance variation. Adding to the terms of Jinks (1954) Hayman included  $F_r = 2 \sum_i d_i h_i \theta_{ri} (1 - w_i^2)$  and  $h = \sum_i h_i (1 - w_i^2)$ , where  $w_i = u_i - v_i$ , already defined,  $\theta_{ri} = 1$  if  $r = i$  and zero otherwise, and there were  $n$  parents with genotypes  $\theta_r = (\theta_{r1}, \theta_{r2}, \dots, \theta_{rn})$  for  $r = 1, \dots, n$ .  $F_r$  was measuring the ratio of dominant to recessive alleles in a single parent  $r$ ; and  $h$  was related to the net direction of dominance.

Nonallelic gene interaction was described as inflating  $H_1/D$ , and depressing  $h^2/H_2$  in the complementary case. In a duplicate type of interaction  $h^2/H_2$  was depressed,  $H_1/D$  and  $H_2/4H_1$  were not changed, and the apparent proportion of dominants was increased. Considering the graph of  $V_r$  (variance of all the offspring of the  $r^{\text{th}}$  parent) and  $w_r$  (covariance between these offspring and their non-recurrent parents), Hayman (1954) stated that epistasis distorted the former case but had no effect in the latter.

Hayman (1957) used a different diallel model for detection of non-allelic interaction. Model components were defined as:

- $m$  = mean such that  $\sum d_r = 0$ ,
- $d_r$  = sum of additive effects of  $r^{\text{th}}$  parent,
- $h_{rs}$  = sum of dominance deviations,
- $p_r$  = mean of  $r^{\text{th}}$  parent,



$f_{rs}$  = mean of the offspring of reciprocal crosses of parents  
r and s, and

$g_{rs}$  = mean of reciprocal  $F_2$  families of the  $F_1$  cross of r and s.

The expectations of the generations follow:

$$\begin{aligned} p_r &= m + d_r, \\ f_{rs} &= m + \frac{1}{2}(d_r + d_s) + h_{rs}, \text{ and} \\ g_{rs} &= m + \frac{1}{2}(d_r + d_s) + \frac{1}{2}h_{rs}. \end{aligned}$$

Weights were assigned as reciprocals of errors determined from replicated P,  $F_1$ , and  $F_2$  means. A fit was made and a  $\chi^2$  was calculated to test for lack of fit, e.g., epistasis. It was noted that in the absence of epistasis  $\hat{h}_{rs} = 2(f_{rs} - g_{rs})$ , but with epistasis  $\hat{h}_{rs}$  contained a term  $y_{rs}$ , the measure of epistasis.

Gardner and Eberhart (1966) discussed the variety cross diallel. The model assumed a diallel cross of random mating varieties, arbitrary gene frequencies, diploid inheritance, no multiple alleles, and no epistasis. As with Hayman (1957) deviations from the model, when a sufficient number of entries are included, were ascribable to epistasis and(or) linkage. When the means of the varieties ( $V_j$ ), the varieties selfed ( $V_j^S$ ), variety crosses ( $C_{jj}$ ), variety crosses selfed ( $C_{jj}^S$ ), and variety crosses random mated ( $C_{jj}^n$ ) were available, the full model described below could be estimated. If four or more varieties were used, then the heterosis parameter  $h_{jj}$ , could be partitioned into average ( $\bar{h}$ ), variety ( $h_j$ ), and specific heterosis ( $s_{jj}$ ). Parameters were  $\mu$ , the mean of random inbred lines from all varieties;  $a_j$ , the contribution of homozygous loci to the  $j^{\text{th}}$  variety mean;  $d_j$ , the contribution of heterozygous loci;  $h_{jj}$ , due to heterosis of

the variety cross caused by differences in gene frequencies or dominance. The means were constituted as shown:

$$\begin{aligned} V_j &= \mu + a_j + d_j, \\ V_j^S &= \mu + a_j + \frac{1}{2}d_j, \\ C_{jj}, &= \mu + \frac{1}{2}(a_j + a_{j'}) + \frac{1}{2}(d_j + d_{j'}) + h_{jj}, \\ C_{jj}^S &= \mu + \frac{1}{2}(a_j + a_{j'}) + \frac{1}{4}(d_j + d_{j'}) + \frac{1}{2}h_{jj}, \text{ and} \\ C_{jj}^r &= \mu + \frac{1}{2}(a_j + a_{j'}) + \frac{1}{2}(d_j + d_{j'}) + \frac{1}{2}h_{jj}. \end{aligned}$$

The authors stated that when only the parents and variety crosses were grown the  $a_j$  and  $d_j$  were confounded and estimated jointly. The new parameters were defined and the analysis shown. Likewise, reduction to general ( $g_i$ ) and specific ( $s_{ij}$ ) effects was shown for the case where parental varieties were not included. In all three cases the models were sequentially fit by least squares and the significance of each additional parameter tested.

Eberhart and Gardner (1966) summarized the situation regarding their variety cross analyses. When the diallel included the variety crosses only, the general and specific combining ability model was appropriate, and no tests for epistasis should be made. Adding the varieties permitted partitioning of heterosis parameters assuming no epistasis, and inclusion of the varieties selfed allowed estimation of all parameters (e.g.,  $a_k$  and  $d_k$  over the previous case).

### Applications of the Methods of Determining Gene Action

A modification of Mather's (1949) scaling test was used by Jinks (1956) on Nicotiana rustica (tobacco) for plant height and flowering time in an 8 x 8 diallel cross. In 10 of 28 crosses in 1952 and 12 of 28 in 1953, significant nonallelic interaction was found for plant height. For flowering time, no crosses in 1952 and 14 of 28 in 1953 showed significant epistasis.

Bauman (1959) applied his test procedure to the characters yield, ear height, and kernel row number in maize. Significant epistatic deviations were found in individual years for each character; however, no significance was shown when the epistasis was combined over 2 years and tested against epistasis x years. In some cases a significant epistasis x years component was found and he concluded that, "epistasis might be similar to or a part of the genotype x environment interaction normally found."

A second application of Bauman's procedure was by Gorsline (1961) in maize. He showed epistasis to be present for all 10 characters. The characters and percent of the material showing epistasis were: yield (38%), moisture (77%), percent silking (85%), stalk quality (62%), plant height (92%), ear height (77%), percent ear node height (85%), ear length (46%), ear diameter (85%), and ear length/ear diameter ratio (85%). Yield and ear length showed fewer occurrences of epistasis than the other characters. The widespread occurrence of epistasis was seen in that all thirteen hybrids showed epistasis for five or more characters. Again significant epistasis x environment interactions were found.

The model of Anderson and Kempthorne (1954) was used by Anderson (1953) on maize data furnished by Stringfield. Six pairs of crosses were

examined for days to mid-silk, ear node height, and yield per acre.

Anderson concluded epistasis was important for all characters because some of the estimates of the epistatic components were as large as or larger than the individual locus effects.

Gamble (1957) examined Anderson and Kempthorne's model as applied to all crosses and derived generations from six inbreds of maize. Hy, WF9, Oh41, B7, B14, and B36 were the inbreds and the following generations were available:  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BC_1$ , and  $BC_2$ . The results showed both nonepistatic and epistatic gene action contributing, but the epistatic contribution was relatively less, especially for yield. Other characters were plant height, kernel row number, ear length, ear diameter, and 100-kernel weight. As with previous results, the combined analysis over years and locations exhibited a decreased importance of epistasis. Anderson (1953) indicated epistasis to be more influenced by environment than locus effects. In particular, B36 contributed much epistasis to all characters, whereas WF9 contributed very little. Further, Anderson commented that epistasis and heterosis showed a "fairly good relation", supporting Hull's (1945) assumption of a relation between hybrid vigor and nonallelic gene interactions.

With the presentation of his generation mean model, Hayman (1958) described five experiments which illustrate the occurrence of epistasis in tobacco, tomato, and wheat. Thompson, Rawlings, and Moll (1963) used Hayman's model to study brown spot resistance in maize. The parents,  $F_1$ ,  $F_2$ ,  $F_3$ ,  $BC_1$ , and  $BC_2$  were used. Deviations from a model including  $m$ ,  $d$ , and  $h$  were nonsignificant and an interpretation of lack of epistasis was made.

Using his 1957 thesis data Gamble (1962a, 1962b) reevaluated for epistasis by Hayman's (1958) method. The particular maize inbreds, generations,

and characters were described earlier in this section. Instead of using a  $\chi^2$  test Gamble appeared to have compared the parameters with their estimated standard errors in determining significance. Dominance effects (d) were positive and as large or larger than the common parameter (m), indicating a very important part of the yield expression was due to dominance. Additive effects were small with 8 of 15 values not significant. All three forms of epistasis (aa, ad, dd) were found with significance for some of the crosses. The additive x additive and additive x dominance effects were of equal importance, with dominance x dominance effects of lesser significance than either of the former two. Epistatic effects generally were more important than additive effects in yield inheritance. Of the remaining five characters (plant height, kernel row number, ear length, ear diameter, and seed weight), all but kernel row number had a major positive contribution by dominance effects. For kernel row number, additive effects were most important. Additive gene effects for other characters were generally significant but of lesser importance than dominance effects. Epistatic effects showed significance for each of the effects for each character in some of the crosses; however, their contributions generally were small relative to additive and dominance effects except for plant height where the epistatic and additive effects were approximately equal. Epistasis was least significant in determining seed weight and only slightly more significant in determining ear diameter, ear length, and kernel row number. A useful summary of significance in Gamble's analysis is in Table 1. The additive effects were equally + and -, dominance effects were +, additive x additive effects generally +, additive x dominance effects equally + or -, and dominance x dominance effects all -.

Table 1. Occurrence of significance (5%) and sign of effects for six characters of the 15 crosses of maize [From Gamble (1962a, 1962b)].

Character	Gene effects										
	m	a		d		aa		ad		dd	
	+	+	-	+	-	+	-	+	-	+	-
Yield	15	6	1	15	0	5	0	3	3	0	3
Plant height	15	6	5	15	0	5	1	6	2	0	8
Kernel row number	15	6	6	9	0	2	3	2	4	0	5
Ear length	15	5	8	15	0	6	0	1	5	0	5
Ear diameter	15	8	4	15	0	3	0	2	7	0	6
Seed weight	15	6	5	15	0	2	0	4	4	0	3

Eberhart and Gardner (1966) also used the data of Gamble (1957) to illustrate the application of their general model. The fit was by least squares and sums of squares were obtained by fitting successive models and taking differences in the reduction sum of squares. The analysis did not include the parents.  $a^*$ , the line component, was calculated as  $a_k + aa_k$ , since  $a_k$  and  $aa_k$  were confounded in the presence of significant additive x additive epistasis. Significance was found for all characters for lines ( $a^*$ ), average heterosis ( $\bar{h}$ ), specific heterosis ( $s$ ), epistasis ( $aa$ ), and deviations from fit. Line heterosis ( $h$ ) was significant for all characters but kernel weight. Significant interactions with locations ( $L$ ) were present in all characters for  $L \times a^*$  and  $L \times \bar{h}$ .  $L \times h$  was significant for all characters but ear length and ear diameter,  $L \times s$  for all but plant height, and  $L \times$  deviations for all but plant height, ear length, and ear diameter.  $L \times$

aa was significant only for kernel row number and ear length. Individual effects were not presented although it was noted that the estimates of  $aa_{kk}$ , were mostly negative for yield.

Turning from effects to variances, Robinson, Comstock, and Harvey (1949) used the Design I mating system to estimate degree of dominance in maize. Little or no dominance was found for plant and ear height. Husk extension showed complete dominance while partial to complete dominance was found for husk score, ear number, ear length, and ear diameter. A suggestion was made that overdominance might have occurred in grain yield. The formula for degree of dominance was that of Comstock and Robinson (1948) where "a" =  $[2(F - M)/M]^{1/2}$ ; F is the females within males mean square, and M is the males mean square. Robinson et al. (1949) stated dominance was complete when "a" = 1; overdominance was indicated by "a" > 1 and partial dominance by "a" < 1.

Design I and Design III experiments were used by Robinson and Comstock (1955) to investigate maize yield. The level of dominance was calculated as  $\hat{\sigma}_D^2/\hat{\sigma}_A^2$  and given for single-cross derived populations and three open-pollinated varieties which had undergone recurrent selection for yield. For the single-cross populations, estimates of the level of dominance were 0.52, 9.26, and 0.69 by Design I and 2.22 (same cross as gave 0.69 from Design I) and 1.27 by Design III. Two of these populations had three cycles of selection with Design I level of dominance estimates of 9.26, 23.00, and 0.01 for the first, and 0.69, 2.24, and 0.0 for the second. The open-pollinated varieties gave Design I estimates of 0.09 and 0.0 for the first variety, 0.75 and 0.22 for the second, and 0.33 for the last. An estimate of 0.0 was inserted due to the estimate of  $\sigma_D^2$  being negative. Two

cycles of selection in the open-pollinated varieties produced changes of 0.09 to 15.50 in one variety and 0.75 to 0.18 in another. Upward bias in the level of dominance resulting from linkage was discussed as contributing to inconsistency in the results. The authors indicated partial to complete dominance for yield in general, with overdominance existing at only a portion of the loci. This statement was indicated as being made considering all the information from their research program.

Eberhart et al. (1966) used combined Design I and II analyses at two levels of inbreeding to estimate genetic components of variance in two open-pollinated varieties of maize, Jarvis and Indian Chief. Characters analyzed were yield, number of ears, ear diameter, ear length, plant height, ear height, and days to tassel after planting. Additive genetic variance accounted for most of the genetic variance for all characters in both varieties. The dominance variance was larger for yield than for other characters. Epistatic variance made little contribution to the total variance, with the exception of yield in the Indian Chief variety. Higher observed standard errors than "expected standard errors" contributed to less significant epistasis than was expected.

Chi (1965) employed covariances among relatives in determining  $\sigma_A^2$ ,  $\sigma_D^2$ , and  $\sigma_I^2$  in an open-pollinated variety of maize. He considered plant height, ear height, kernel row number, ear length, ear diameter, yield, and 300-kernel weight.  $\hat{\sigma}_{AAA}^2$  was included in  $\hat{\sigma}_I^2$  which was negligible in relation to other variance components. Most of the genetic variance was  $\hat{\sigma}_A^2$ , but the proportion of  $\hat{\sigma}_A^2$  and  $\hat{\sigma}_D^2$  was variable.  $\hat{\sigma}_A^2$  was greatest for ear height and length, kernel row number, and 300-kernel weight.  $\hat{\sigma}_D^2$  was greater than  $\hat{\sigma}_A^2$  for plant height, ear diameter, and yield.



Single and three-way crosses of maize were analyzed by Wright (1966) using diallel and triallel analyses. His object was to estimate the genetic variance components and their interaction with environment in an open-pollinated variety. From the diallel analysis he found significant  $\sigma_A^2$  and  $\sigma_D^2$  for plant height, ear height, ear length, ear diameter, kernel row number, date silk, yield, and 300-kernel weight. The triallel analysis indicated significant amounts of  $\sigma_I^2$  for all characters.  $\sigma_{A \times E}^2$  was present for all characters, and  $\sigma_{I \times E}^2$  was present in most characters but less than  $\sigma_{A \times E}^2$ . Wright concluded that additive type epistatic effects were of greater importance than dominance effects and that  $\sigma_A^2$  accounted for the majority of  $\sigma_G^2$  present in this open-pollinated variety.

Jinks (1955) reanalyzed the data of Kinman and Sprague (1945) and showed evidence of nonallelic interaction in maize yield for the 10 x 10 diallel cross. Overdominance was associated with nonallelic interaction, e.g., omission of crosses showing nonallelic interaction lowered the amount of overdominance. He stated specific combining ability (s.c.a.) was associated with the presence of nonallelic interactions and general combining ability (g.c.a.) was the result of simple dominance. (Note that g.c.a. is associated with the average performance of a line in all crosses while s.c.a. is the deviation of a specific cross from the average performance of its parents.)

## MATERIALS AND METHODS

## Inbred Lines

Twenty-two maize inbred lines were chosen for this study. They represent four Types as defined below:

Type I = lines isolated from open-pollinated varieties  
or 1<sup>st</sup> Cycle lines,

Type II = lines isolated from segregates of planned crosses  
and synthetic varieties or 2<sup>nd</sup> Cycle lines,

Type III= "good" lines with respect to agronomic traits  
and combining ability,

Type IV = "poor" lines with respect to agronomic traits  
and combining ability.

The "good" lines, as opposed to "poor" lines, were selected as having lower plant and ear height, earlier flowering, larger ears, higher yield, less lodging, and a generally more acceptable appearance by the standards of the maize breeding trade. "Good" lines were also thought to perform better in combination with other lines with respect to general combining ability.

Some of the lines were multiply classified among the four Types. These were treated as separate entities throughout the experiment. In all, seven lines were assigned to each Type to obtain balance. The inbred lines, Types, and sources [Henderson (1964)] of the inbreds are in Table 2.

A diallel crossing pattern was employed to obtain 21  $F_1$ 's within each Type starting in 1963. In subsequent years the  $F_2$ ,  $F_3$ , backcrosses to both parents( $BC_1$ ,  $BC_2$ ), and backcrosses selfed ( $BS_1$ ,  $BS_2$ ) were obtained for each  $F_1$  cross. A complete listing of the  $F_1$  crosses by Types is in Table 66.

Each generation had 21 entries for each Type considering BC<sub>1</sub>, BC<sub>2</sub>, BS<sub>1</sub>, and BS<sub>2</sub> separately. In 1966 and 1967 the parents, F<sub>1</sub>'s, F<sub>2</sub>'s, BC<sub>1</sub>'s, and BC<sub>2</sub>'s were remade in sufficient quantity to plant the experiment the following year.

Table 2. Classification and source of inbred lines.

Inbred	Type(s)	Source
38-11	I	Funk 176A
WF9	I	Wilson Farm Reid Yellow Dent
Hy	I	Illinois High Yield
L317	I	Lancaster Sure Crop
L289	I, IV	Lancaster Sure Crop
I205	I	Iodent
I159	I	Iodent
A619	II, III	(A171 x Oh43) Oh43
B14	II	Iowa Stiff Stalk Synthetic
B37	II	Iowa Stiff Stalk Synthetic
(B38 x B217)Selected	II, III	B38 x B217
B50	II, III	(M14 x A206) Oh4c
B54	II, IV	Iowa Corn Borer Synthetic #1
B55	II, III	(Oh45 x W92)Selected
B46	III	(W22 x B10)Selected
B53	III	W24 x B2
B57	III	Midland-125-2-1
B38	IV	(H0 x B10 <sup>2</sup> )Selected
B39	IV	Iowa Stiff Stalk Synthetic
B44	IV	Iowa Stiff Stalk Synthetic
B52	IV	MR164
R177	IV	Snelling Corn Borer Synthetic

## Field Procedures

The study was grown at Ames, Ankeny, and Martinsburg, Iowa, in 1968 and 1969. Due to extreme moisture and resultant stunting of plants, the 1969 Ankeny material was discarded prior to any data being taken. The remaining five location-year combinations have been designated as five random environments as in Table 3.

The experimental design was a 9 x 10 simple rectangular lattice for each generation. Six checks from a bulk of that generation's seed were added to the 84 entries (4 Types x 21 entries within a Type) to bring the total entries in a generation to 90. The inbred parental generation (P), unlike the others, had 28 entries since the same parent in different Types was kept separate. Thus each parent was entered three times to give 84 entries plus six late maturing inbred checks for a total of 90.

Entries were assigned entry numbers at random for each of the eight generations. While there was a  $P_1$  and  $P_2$  for each particular  $F_1$ , these were not distinguished until application of the generation mean analysis. Block numbers were randomly assigned in each replication and the order of entries within a block was also randomized. In order to avoid soil differences between generations which could occur if each generation was treated as a separate experiment in the field, a block from each generation was chosen and a group of 72 entries (8 generations x 9 entries per block in each of the 8 generations) were associated as 8 blocks of 9 plots. There were 10 such groups of 72 entries each, constituting the 720 entries per replication. Ordering of the generations in these 10 groups was also at random.

To avoid the competition effect of generations, the nine entries in a

given block were bordered by a single row on each side made up from a bulk of the seed in the particular generation. Thus, a given block from a given generation went into the field as 11 plots; the nine entries plus two border rows. Plots were overplanted and thinned to 17 single-plant hills. Row spacings, plant spacings, and plant densities are shown in Table 3. Missing hills were filled in with a purple marker to provide competition. Data were taken on the first 10 competitive plants in each plot. Plots with less than four competitive plants were considered missing and their treatment is described in the section on statistical procedures.

Eight quantitative characters were considered. Date of silk was taken as days from July 1 until 50% of the plants in a plot showed silk. These data were obtained only at the Ames location. Plant height, in centimeters, was measured from the ground to the collar of the topmost leaf, and ear height from the ground to the node of the upper ear. Both were measured after pollen shed. The ears were harvested and dried in forced-air dryers. Counts of number of kernel rows were taken near the butt of the ear. Ear length and diameter were measured in centimeters. The ears were then shelled and the yield of shelled corn weighed to the nearest gram. A random sample of 300 kernels was taken and their weight determined to the nearest decigram. Ears from plants which produced more than one ear were kept together and the second ear was disregarded for kernel row number, ear length, and ear diameter measurements. All ears were shelled together for yield and sampled for 300-kernel weights. Plot means were calculated for all characters except date of silk and 300-kernel weight.

Table 3. Field information on the five environments.

Characteristic	Environment 1	Environment 2	Environment 3	Environment 4	Environment 5
Year	1968	1968	1968	1969	1969
Location	Ames	Ankeny	Martinsburg	Ames	Martinsburg
Date planted	April 27	May 10	May 3	May 16	May 27
Row spacing (cm)	76.2	91.4	96.5	76.2	96.5
Plant spacing (cm)	30.5	24.1	22.9	30.2	22.9
Plants per hectare	42,995	45,321	45,321	43,415	45,321
Previous crop	Oats	Corn	Soybeans	Oats	Soybeans
Fertilizer (kg/ha)					
Total $\text{NH}_4\text{NO}_3$	168	199	184	168	231
Total $\text{NH}_3$					168
Total $\text{P}_2\text{O}_5$	90	124	62	112	195
Total $\text{K}_2\text{O}$	90	124	57	112	176

## Statistical Procedures

Lattice analysis

A simple rectangular lattice analysis of variance was performed on each generation in each environment with the aid of an IBM 360/65 computer at the Iowa State University Computation Center. The adjusted means and effective error mean squares were obtained for further use in the generation mean analysis. Cochran and Cox (1968) gave the following formulae for adjustment of treatment totals which may be divided by  $r = 2$  to obtain adjusted means:

$B$  = block totals in replicate  $X$  and replicate  $Y$ ,

$r = 2$  = number of replications,

$k$  = block size = 9 in this case,

$E_b$  = block error mean square from the AOV,

$E_e$  = intrablock error mean square from the AOV,

$C$  = total (over all replications) of all treatments in a block -  $rB$ , where  $C$  is calculated for each block in each replication,

$S$  = sum of  $C$  values over replications for partners, e.g., those  $C$  values with the same block number such as  $X_2$  and  $Y_2$ ,

$$\lambda = \frac{r(E_b - E_e)}{r(k - 1)E_b + (rk - 2k + r)E_e},$$

$$\mu = \frac{r(E_b - E_e)}{r(k + 1)E_b + (rk - 2k - r)E_e},$$

Adjustment factor for a block in a given replication =  $\lambda C - \mu S$  where  $S$  is for the given block and  $C$  is for the given block and replication,

Adjusted treatment totals = unadjusted treatment total  
+ adjustment factors for every block in which the  
treatment appears in each replicate. Note that  
there are two adjustment factors for each treatment  
total in the simple rectangular lattice case.

A formula for the effective error mean square was given by Robinson

and Watson (1949) as  $\frac{2E_e}{r} \left[ 1 + \frac{2k^2\lambda}{(k^2 + k - 1)} - \mu \right]$  and was termed "approximate

mean variance of all comparisons" by them.

Missing plots fell into four categories: (1) an entry was missing in one replicate but present in the other, and the generation was not parental; (2) the missing entry was from the parental generation and one or two of the three entries of that inbred in a replicate were missing; (3) all three entries of an inbred were missing in a replicate; and (4) plots in both replicates of a given entry or inbred were missing. The latter case occurred six times, three with Type IV inbreds and three times where no seed was found for an  $F_2$  entry in 1968.

Unfortunately more missing plots occurred in some environments than could be reasonably estimated by covariance reiteration techniques. As such, case (1) above was handled by taking the value of the corresponding entry in the other replicate as the missing plot value. In case (2) an average of the entries for the same inbred within that replicate was used as the missing plot value while in case (3) the average of entries of the same inbred in the second replicate was used for all three missing plots in the first. For case (4) a rough estimate was made, and the generation mean analysis with one reiteration was used to predict the missing plot value.

All missing plot calculations were made before running the lattice



analysis. The degrees freedom for the effective error mean square were adjusted for missing plots and a corrected error mean square was calculated for use in t-tests.

To increase the accuracy of the inbred observed values, the three duplications of each inbred were averaged once the adjusted means were obtained and the variance of an inbred mean reduced accordingly.

A correspondence was established between entry numbers and crosses for the generation mean analysis. Each entry derived from a particular  $F_1$  cross was given the same cross-code number. Parents of the cross were also assigned that same code number. Thus there were nine entries consisting of two parents ( $P_1$  and  $P_2$ ), the  $F_1$ ,  $F_2$ ,  $BC_1$ ,  $BC_2$ ,  $BS_1$ , and  $BS_2$  for each cross-code number in each environment. By assigning each of the nine generations a number code it was then possible to completely sort the data into Types (I-IV), crosses (1-84), environments (1-5), and generations (1-9). All checks were discarded at this point.

#### Generation mean analysis

The generation mean analysis of Hayman (1958) was applied to each cross in each environment for each character. Gamble's (1962a) notation was used in defining parameters since the meaning is more readily apparent. Two models were fit by least squares independently: Model 1 consisting of  $m$ ,  $a$ , and  $d$ ; and Model 2 consisting of  $m$ ,  $a$ ,  $d$ ,  $aa$ ,  $ad$ , and  $dd$ . A fit was made for each environment as well as a combined fit over all five environments. Predicted values were computed for each fit.

In matrix notation the parameters are related to generations as follows:

$$\begin{array}{l}
 \left( \begin{array}{c} F_1 \\ F_2 \\ F_3 \\ BC_1 \\ BC_2 \\ BS_1 \\ BS_2 \\ P_1 \\ P_2 \end{array} \right) = \left( \begin{array}{cccccc} 1.0 & 0.0 & 0.5 & 0.0 & 0.0 & 0.25 \\ 1.0 & 0.0 & 0.0 & 0.0 & 0.0 & 0.0 \\ 1.0 & 0.0 & -0.25 & 0.0 & 0.0 & 0.0625 \\ 1.0 & 0.5 & 0.0 & 0.25 & 0.0 & 0.0 \\ 1.0 & -0.5 & 0.0 & 0.25 & 0.0 & 0.0 \\ 1.0 & 0.5 & -0.25 & 0.25 & -0.25 & 0.0625 \\ 1.0 & -0.5 & -0.25 & 0.25 & 0.25 & 0.0625 \\ 1.0 & 1.0 & -0.5 & 1.0 & -1.0 & 0.25 \\ 1.0 & -1.0 & -0.5 & 1.0 & 1.0 & 0.25 \end{array} \right) \left( \begin{array}{c} m \\ a \\ d \\ aa \\ ad \\ dd \end{array} \right).
 \end{array}$$

This may be designated as  $Y = X\beta$ , where  $Y$  is the column of observations,  $X$  is the matrix of coefficients, and  $\beta$  is the column of parameters. Note that Model 1 consists of the first three columns of the coefficient matrix,  $X$ , and  $m$ ,  $a$ , and  $d$  of the parameters while Model 2 is as above. The normal equations were obtained as  $X'Y = X'X\beta$ , and the solution as  $[X'X]^{-1} X'Y = \hat{\beta}$ . The inverse matrices for both models are shown below:

Model 1

$$[X'X]^{-1} = \begin{pmatrix} 0.1364 & 0.0 & 0.1818 \\ 0.0 & 0.3333 & 0.0 \\ 0.1818 & 0.0 & 1.3091 \end{pmatrix}$$

Model 2

$$[X'X]^{-1} = \begin{pmatrix} 0.2336 & 0.0 & 0.0376 & -0.1101 & 0.0 & -0.7732 \\ 0.0 & 1.6190 & 0.0 & 0.0 & 1.7143 & 0.0 \\ 0.0376 & 0.0 & 3.9141 & 3.1087 & 0.0 & -5.0899 \\ -0.1101 & 0.0 & 3.1087 & 3.7530 & 0.0 & -6.8081 \\ 0.0 & 1.7143 & 0.0 & 0.0 & 2.2857 & 0.0 \\ -0.7732 & 0.0 & -5.0899 & -6.8081 & 0.0 & 22.4215 \end{pmatrix}.$$

The sum of squares due to regression (SSR) is  $\hat{\beta}'X'Y$  and the total uncorrected sum of squares equals  $Y'Y$ . A residual is obtained as  $Y'Y - \hat{\beta}'X'Y$ . The reduction due to  $m$ ,  $R(m)$ , was subtracted from the SSR and total sum of squares in the analyses presented. Note that  $R(m)$  obtained when  $m$  alone is fit is in fact the usual correction for the mean. Predicted values were

calculated as  $\hat{Y} = X\hat{\beta}$  for each model.

The analyses for one environment are outlined in Tables 4 and 5.

Table 4. Analysis of variance by Model 1 for a given cross in one environment.

Source	df	Sum of squares
a, d	2	$\hat{\beta}'X'Y - R(m) = R(a, d)$
Residual	6	$Y'Y - \hat{\beta}'X'Y$
Total	8	$Y'Y - R(m)$

Table 5. Analysis of variance by Model 2 for a given cross in one environment.

Source	df	Sum of squares
a, d, aa, ad, dd	5	$\hat{\beta}'X'Y - R(m) = R(a, d, aa, ad, dd)$
Deviation	3	$Y'Y - \hat{\beta}'X'Y$
Total	8	$Y'Y - R(m)$

F-tests for these two analyses were made using the lattice effective error mean squares pooled across the eight generations for the particular environment. The reduction due to fitting aa, ad, and dd was calculated as  $R(a, d, aa, ad, dd) - R(a, d)$ . The combined analyses over environments were computed similarly without fitting any environmental effects. By using the individual analyses in each environment and the combined analysis over environments the interaction of effects with environments were

obtained. Table 6 gives the method by which these were calculated. In Table 6 the subscript c refers to the combined analysis, while values without subscripts refer to individual environments. M1 and M2 are used to designate Model 1 and Model 2, respectively, and  $y_{ic}$  is the average over five environments of the  $i^{\text{th}}$  generation. (Note: Since environmental ef-

Table 6. Analysis of variance for a given cross combined over the five environments.

Source	df	Sum of squares	
Environments	4	$S_{10} - S_6 - S_1$	
Generations	8	$5\sum_i (y_{ic} - \bar{y}_{ic})^2$	= $S_1$
a, d	2	$\hat{\beta}'X'Y_{M1c} - R(m)_c$	= $S_2$
Residual	6	$S_1 - S_2$	= $S_3$
Epistasis	3	$\hat{\beta}'X'Y_{M2c} - \hat{\beta}'X'Y_{M1c}$	= $S_4$
Deviations	3	$S_3 - S_4$	= $S_5$
Env. x Gen.	32	$S_7 + S_8$	= $S_6$
Env. x a, d	8	$\sum_{\text{Env.}} [\hat{\beta}'X'Y - R(m)] - S_2$	= $S_7$
Env. x Res.	24	$\sum_{\text{Env.}} (Y'Y - \hat{\beta}'X'Y_{M1}) - S_3$	= $S_8$
Env. x Epi.	12	$\sum_{\text{Env.}} (\hat{\beta}'X'Y_{M2} - \hat{\beta}'X'Y_{M1}) - S_4$	= $S_9$
Env. x Dev.	12	$S_8 - S_9$	
Pooled Dev.	15	$S_5 + S_9$	
Pooled error		From lattice analyses as described	
Total	44	$Y'Y_c - R(m)_c$	= $S_{10}$

fects were not included, only nine predicted values were obtained, hence the reason for a  $y_{ic}$  term for observed values in the combined analysis; however,  $Y'Y_c$  was based on 45 observations from the individual environments.) Epistasis refers to the reduction due to aa, ad, and dd. A pooled error was computed from the effective error mean squares of the lattice analysis for testing the interactions while main effects were tested against their respective interactions. In calculating the pooled error, the individual errors for the eight generations in a given environment were pooled and then these were pooled across environments. The analysis for date silk which was taken in only two environments must be modified slightly from the one shown above.

Analyses were pooled over the 21 crosses in a Type by averaging the mean squares and multiplying the degrees of freedom by 21. This was done for analyses in a single environment and for the combined analyses.

A second method of examination was to test the individual effects, and differences between effects pooled over crosses in Types. The individual effects and differences were tested using a t-test with the appropriate standard error calculated by pooling errors from the lattice analyses. For instance, the test for the existence of an aa effect pooled over crosses in a Type and combined over environments is:

$$t = \frac{\sum_{\text{crosses}} \hat{a}_a c / 21}{SE} \quad \text{where } SE = \left[ c_{kk} s^2 / 105 \right]^{1/2}$$

$s^2$  is the pooled error from the combined analysis of variance and  $c_{kk} = 3.7530$  is the element for the variance of aa from the inverse matrix of Model 2.

Standard errors used are shown below where  $s_j^2$  is the pooled error for

a cross in a given environment obtained as previously described, and  $c_{kk}$  is the diagonal element from the M1 or M2 inverse for the effect to be tested.

<u>SE of</u>	<u>SE</u>
Effect in a given environment j	$(c_{kk}s_j^2)^{1/2}$
Effect pooled over crosses in a Type in a given environment	$(c_{kk}s_j^2/21)^{1/2}$
Effect combined over environments	$(c_{kk}s^2/5)^{1/2}$
Effect combined over environments and pooled over crosses in a Type	$(c_{kk}s^2/105)^{1/2}$

Standard errors for differences may be obtained by multiplying the above values by  $\sqrt{2}$ .

The last procedure used was product-moment correlation. In each environment for one cross there are nine observed values and 18 predicted values, nine by each model. Considering the five environments there are five sets of observed values and 10 sets of predicted values leading to a 15 x 15 correlation matrix. Since there are 21 crosses in a Type and nine values (generations) for a cross, an n of 189 was used and the 15 x 15 correlation matrix computed for each Type within each character.

Summarization of the data was aided immeasurably by having the regression analyses for each environment, the combined analysis for each cross, and all observed and predicted values put on a disk pack. The direct access feature enabled tables to be made pulling out only the desired values and operating with them. Such procedure is to be recommended for summarizing any experiment of this size where many repetitive

operations are involved.

The maximum possible number of individual plant observations, assuming no missing plots, was:

Number of individual plant observations = 5 characters  
x 10 observations per entry x 720 entries per replicate  
x 2 replicates x 5 environments + 2 characters x 1  
observation per entry x 720 x 2 x 5 + 1 character x 1  
observation per entry x 720 x 2 x 2 environments =  
377,200.

## EXPERIMENTAL RESULTS

Environment 1 suffered some wind damage prior to flowering, but otherwise was satisfactory. Environment 3, and environment 2 to a lesser extent, lacked moisture at silking and during grain filling, which resulted in some barrenness and small ears. Environment 4 was ideal until just before harvest when hail and high wind caused leaf tearing and root lodging. The ears had filled by that time, so the only result was the inconvenience in hand harvesting lodged plants. Environment 5 had too much moisture early in the season, causing some stunting of plants in wet areas of the field. Conditions at flowering and later were less than desired, but still acceptable.

The effective error mean squares from the simple rectangular lattice analysis of variance are shown in Table 7. Errors on the parent generation (P) may seem low; however, as indicated previously, the three duplications of each inbred line were averaged, reducing the error of an individual mean. Environment 5 showed relatively large errors for plant height, ear height, and ear length when compared to the other four environments. There was a tendency for the  $F_3$  errors to be largest, while  $F_1$  errors were smallest, excluding the parental generation. Yield did not follow this pattern. The  $F_1$  errors for yield were larger than for any other generation in four of five environments. The large  $F_3$  errors reflected different effects of inbreeding depression among the 84 crosses. An unusually large difference between the backcross selfed ( $BS_1$  and  $BS_2$ ) generations for yield in environment 1 was noted; however, the difference was in the same direction in three of the remaining four environments.



Table 7 also contains degrees of freedom for the errors. A maximum of 71 was possible if there were no missing plots. The P, F<sub>3</sub>, BS<sub>1</sub>, and BS<sub>2</sub> generations were most susceptible to missing plots, in roughly that order. Environments 2 and 3 were particularly bad for ear traits.

When the errors of Table 7 were pooled across the eight generations, the result was an error applicable to a given cross in a given environment for a particular character, or character-environment error. These are shown in Table 8. Previous comments regarding the high variation in environment 5 are applicable. Proceeding a step further, the errors of Table 8 were pooled across environments, resulting in an error for a given cross and a particular character as shown in Table 9.

Effective selection of inbreds for each Type was a prerequisite in determining different types of gene action. Confirmation of success is demonstrated in Table 10. Both the midparent and F<sub>1</sub> observed values are shown pooled over environments and crosses in a Type. The differences between Type I versus Type II and Type III versus Type IV were highly significant for all characters in the midparent comparisons. Considering the F<sub>1</sub> means, all characters for the second comparison (Type III vs. Type IV) showed significant differences, while all but kernel row number and ear length were significant for the first comparison (Type I vs. Type II). Thus, Type II inbreds compared to Type I, had earlier maturity, shorter plants, lower ears, more kernel rows, larger ears, higher yields, and heavier kernels. Type III versus Type IV inbreds showed Type III to have earlier maturity, shorter plant and ear height, more kernel rows, longer and larger diameter ears, higher yield, and lighter kernels. Except for kernel weight, this was in line with the description of "good" as opposed

Table 7. Effective error mean squares from the lattice analyses on a per mean basis.

Character Generation	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
	MS	df	MS	df	MS	df	MS	df	MS	df
Date silk										
F <sub>1</sub>	0.5964	71					0.6117	71		
F <sub>2</sub>	1.5160	69					0.9310	71		
F <sub>3</sub>	2.3285	70					1.3393	71		
BC <sub>1</sub>	1.0952	70					0.8198	70		
BC <sub>2</sub>	0.9794	69					1.0095	71		
BS <sub>1</sub>	1.4675	71					2.0044	71		
BS <sub>2</sub>	1.4254	70					0.9460	71		
P	0.4449	64					0.4284	71		
Plant height										
F <sub>1</sub>	21.7531	71	13.8640	71	15.5833	71	17.8180	71	52.7150	70
F <sub>2</sub>	36.7789	68	28.2970	69	21.5403	69	26.9863	71	61.9355	69
F <sub>3</sub>	30.7344	70	29.1883	71	25.1377	71	32.9316	71	88.2776	70
BC <sub>1</sub>	27.9509	70	23.2121	71	17.3637	71	16.3889	71	72.8826	70
BC <sub>2</sub>	20.6897	69	22.6072	71	29.9651	71	22.1129	71	57.8801	71
BS <sub>1</sub>	25.9858	71	23.8999	71	33.3529	71	27.4258	71	55.3196	71
BS <sub>2</sub>	27.2587	70	20.0394	71	29.5880	71	24.5549	71	56.8193	71
P	5.6461	64	4.0958	71	7.2248	71	6.6091	71	28.8219	70

Table 7. (Continued)

Character Generation	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
	MS	df	MS	df	MS	df	MS	df	MS	df
Ear height										
F <sub>1</sub>	10.0095	71	12.6274	71	9.4563	71	7.7141	71	28.5301	70
F <sub>2</sub>	19.4772	68	19.8711	69	13.9188	69	21.4235	71	28.0520	69
F <sub>3</sub>	24.1582	70	22.5264	71	11.6791	71	19.9884	71	33.1766	71
BC <sub>1</sub>	18.6806	70	15.4010	71	12.3051	71	15.7868	71	49.7303	70
BC <sub>2</sub>	13.2016	69	16.9240	71	12.7607	71	14.2941	71	30.0044	71
BS <sub>1</sub>	14.8266	71	16.5062	71	13.8435	71	20.3210	71	36.1047	70
BS <sub>2</sub>	18.0605	70	20.3788	71	17.6500	71	20.1440	71	28.3646	71
P	3.9093	64	2.3153	71	2.4556	71	6.5341	71	9.2895	67
Kernel row no.										
F <sub>1</sub>	0.1605	70	0.1758	71	0.1630	71	0.2231	71	0.2483	70
F <sub>2</sub>	0.2676	66	0.3327	69	0.3656	68	0.3422	71	0.2753	68
F <sub>3</sub>	0.3239	67	0.2784	67	0.2943	58	0.2464	71	0.3896	68
BC <sub>1</sub>	0.2380	68	0.2201	71	0.2664	70	0.2728	71	0.2709	70
BC <sub>2</sub>	0.2477	65	0.3220	71	0.2580	70	0.2129	71	0.4040	70
BS <sub>1</sub>	0.2657	69	0.2862	67	0.3548	61	0.3273	70	0.2834	71
BS <sub>2</sub>	0.2716	66	0.3927	68	0.3074	61	0.5355	71	0.2329	70
P	0.0817	59	0.1482	41	0.2152	23	0.1030	69	0.1695	56

Table 7. (Continued)

Character Generation	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
	MS	df	MS	df	MS	df	MS	df	MS	df
Ear length										
F <sub>1</sub>	0.2719	70	0.2989	71	0.4659	71	0.5649	71	1.5602	70
F <sub>2</sub>	0.4988	66	0.5239	69	0.4537	68	0.7789	71	1.0230	68
F <sub>3</sub>	0.4662	67	0.3551	67	0.6159	58	0.6127	71	1.3053	68
BC <sub>1</sub>	0.4887	68	0.3293	71	0.4250	70	0.5646	71	1.1930	70
BC <sub>2</sub>	0.6699	65	0.3470	71	0.7091	70	0.5828	71	1.2256	70
BS <sub>1</sub>	0.6111	69	0.3120	67	0.5893	61	0.6375	70	1.0039	71
BS <sub>2</sub>	0.4594	66	0.5330	68	0.7648	61	0.5261	71	1.0250	70
P	0.1440	59	0.2500	41	0.2497	23	0.3100	69	0.4889	56
Ear diameter										
F <sub>1</sub>	0.0058	70	0.0090	71	0.0101	71	0.0137	71	0.0139	70
F <sub>2</sub>	0.0116	66	0.0072	69	0.0123	68	0.0147	71	0.0165	68
F <sub>3</sub>	0.0116	67	0.0116	67	0.0151	58	0.0130	71	0.0212	68
BC <sub>1</sub>	0.0086	68	0.0092	71	0.0131	70	0.0141	71	0.0194	70
BC <sub>2</sub>	0.0082	65	0.0086	71	0.0120	70	0.0139	71	0.0142	70
BS <sub>1</sub>	0.0114	69	0.0112	67	0.0145	61	0.0148	70	0.0235	71
BS <sub>2</sub>	0.0105	66	0.0123	68	0.0173	61	0.0138	71	0.0170	70
P	0.0063	59	0.0086	41	0.0083	23	0.0045	69	0.0087	56

Table 7. (Continued)

Character Generation	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
	MS	df	MS	df	MS	df	MS	df	MS	df
Yield										
F <sub>1</sub>	124.1117	70	142.2711	71	197.6095	71	228.6455	71	249.1880	70
F <sub>2</sub>	137.5303	66	118.2773	69	111.2448	68	158.7280	71	156.9081	68
F <sub>3</sub>	235.8887	67	103.3324	67	116.3600	58	138.8308	71	122.6386	68
BC <sub>1</sub>	133.7133	68	137.1956	71	145.7018	69	133.0465	71	187.8771	69
BC <sub>2</sub>	132.1323	64	102.5628	71	163.8066	70	141.2313	71	201.5859	69
BS <sub>1</sub>	125.0096	67	122.9128	67	147.2319	61	99.7771	70	124.9519	70
BS <sub>2</sub>	232.5780	66	157.4925	68	173.3000	61	117.7575	71	98.9646	70
P	39.9451	59	55.7972	40	55.6558	23	40.9557	69	28.8679	56
300-kernel wt.										
F <sub>1</sub>	14.0038	70	17.7111	71	15.5340	71	17.5090	69	18.1222	70
F <sub>2</sub>	15.0394	65	23.0862	69	21.1265	68	23.7536	71	21.0174	67
F <sub>3</sub>	19.6316	67	18.1111	67	22.0127	58	20.7734	70	23.9800	68
BC <sub>1</sub>	21.5172	68	26.0778	71	17.7249	69	19.3365	69	21.3390	70
BC <sub>2</sub>	18.2325	64	22.3080	71	16.1953	70	19.9751	71	26.3553	68
BS <sub>1</sub>	22.7186	66	15.7196	67	19.4017	61	22.9744	70	20.8377	71
BS <sub>2</sub>	18.6799	66	24.7783	68	22.3127	61	22.1423	70	24.1669	70
P	6.2101	59	16.5566	40	15.4754	23	11.2447	67	12.3524	56

Table 8. Effective errors from the lattice analysis pooled over generations for a character in a given environment ( $s_j^2$ )

Character	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
	$s_1^2$	df	$s_2^2$	df	$s_3^2$	df	$s_4^2$	df	$s_5^2$	df
Date silk	1.2394	554					1.0116	567		
Plant height	24.7657	553	20.6234	566	22.4727	566	21.8534	568	59.3126	562
Ear height	15.3921	553	15.8044	566	11.7510	566	15.7757	568	30.5246	559
Kernel row no.	0.2339	530	0.2753	525	0.2812	482	0.2853	565	0.2858	543
Ear length	0.4546	530	0.3744	525	0.5547	482	0.5730	565	1.1183	543
Ear diameter	0.0093	530	0.0097	525	0.0131	482	0.0128	565	0.0170	543
Yield	146.4911	527	120.9638	524	146.9774	481	132.7528	565	149.2888	540
300-kernel wt.	17.1464	525	20.8009	524	18.8637	481	19.7716	557	21.2150	540

Table 9. Effective errors from the lattice analysis pooled over generations and environments for a given character ( $s^2$ ).

Character	$s^2$	df
Date silk	1.1212	1121
Plant height	29.7813	2815
Ear height	17.8279	2812
Kernel row no.	0.2722	2645
Ear length	0.6185	2645
Ear diameter	0.0124	2645
Yield	139.1366	2637
300-kernel wt.	19.5827	2627

to "poor" inbreds presented in the section describing the inbred lines used.

A measure of inbreeding depression,  $MP/F_1$ , is also given in Table 10. The values for date silk are of little absolute meaning since July 1<sup>st</sup> was an arbitrary starting point. Type IV had the largest depression on inbreeding for all characters but 300-kernel weight. The least depression, generally, occurred for 300-kernel weight and the most for yield. Plant height loss was most uniform among the four Types, while yield had a difference of 0.20 between the ratios of Type III and IV.

The remainder of the results may be divided into three broad categories: regression analyses, tests of individual effects, and correlation analyses.

Table 10.  $F_1$  and midparent (MP) observed values and standard deviations (SD) pooled over environments and crosses within a Type; and the ratio of midparent to  $F_1$  as a measure of inbreeding depression.

Character Type	MP	SD(MP)	$F_1$	SD( $F_1$ )	MP/ $F_1$
Date silk					
Type I	36.59	0.07	29.40	0.12	1.24
Type II	34.12	0.07	27.55	0.12	1.24
Type III	33.51	0.07	28.05	0.12	1.19
Type IV	37.28	0.07	29.92	0.12	1.25
Plant height					
Type I	169.81	0.22	227.32	0.48	0.75
Type II	152.99	0.22	210.35	0.48	0.73
Type III	152.72	0.22	203.65	0.48	0.75
Type IV	157.53	0.22	221.99	0.48	0.71
Ear height					
Type I	85.31	0.15	115.99	0.36	0.74
Type II	57.99	0.15	90.84	0.36	0.64
Type III	60.26	0.15	89.05	0.36	0.68
Type IV	63.90	0.15	99.94	0.36	0.64
Kernel row no.					
Type I	14.16	0.02	15.84	0.04	0.89
Type II	14.45	0.02	15.78	0.04	0.92
Type III	14.73	0.02	16.41	0.04	0.90
Type IV	13.26	0.02	15.63	0.04	0.85



Table 10. (Continued)

Character Type	MP	SD(MP)	F <sub>1</sub>	SD(F <sub>1</sub> )	MP/F <sub>1</sub>
Ear length					
Type I	12.59	0.04	18.38	0.08	0.69
Type II	14.67	0.04	18.19	0.08	0.81
Type III	14.66	0.04	18.22	0.08	0.80
Type IV	12.72	0.04	19.25	0.08	0.66
Ear diameter					
Type I	3.81	0.01	4.57	0.01	0.83
Type II	4.00	0.01	4.71	0.01	0.85
Type III	4.01	0.01	4.62	0.01	0.87
Type IV	3.66	0.01	4.55	0.01	0.80
Yield					
Type I	48.61	0.45	152.65	1.34	0.32
Type II	63.57	0.45	159.59	1.34	0.40
Type III	67.03	0.45	150.72	1.34	0.44
Type IV	38.23	0.45	158.47	1.34	0.24
300-kernel wt.					
Type I	63.37	0.24	76.07	0.40	0.83
Type II	71.76	0.24	82.52	0.40	0.87
Type III	67.72	0.24	72.57	0.40	0.93
Type IV	73.46	0.24	76.40	0.40	0.96

### Regression Analyses

Each cross and related generations were analyzed in each environment for each character by fitting  $m$ ,  $a$ , and  $d$  as Model 1 and  $m$ ,  $a$ ,  $d$ ,  $aa$ ,  $ad$ , and  $dd$  as Model 2. The fit was by unweighted least squares. Sums of squares examined were: the reduction due to fitting  $a$  and  $d$  after  $m$ ; the residual after fitting  $m$ ,  $a$ , and  $d$ ; the reduction due to fitting  $aa$ ,  $ad$ , and  $dd$  after  $m$ ,  $a$ , and  $d$ ; and the deviations after fitting all of Model 2. For convenience, the term "residual" will be used in conjunction with Model 1 and the term "deviations" will be used with Model 2. These sums of squares were all tested against the appropriate pooled error ( $s_j^2$ ) from Table 8. Counts of the occurrence of significance were made for the 21 crosses in each Type and the results are in Tables 11 through 18.

Partitioning of the residual after fitting  $m$ ,  $a$ , and  $d$  into epistasis and deviations nearly always brought out more total cases of significance than indicated by the occurrence of a significant residual. There was wide variation in the occurrence of epistasis from environment to environment for some of the Types. It often occurred that all Types were higher or lower in a given environment. All characters except kernel row number and 300-kernel weight had nearly 21 of 21 crosses significant for the reduction due to fitting  $a$  and  $d$ .

Type I had more cases of significant epistasis and deviations for date silk and ear length than did Type II. Types I and II had roughly equal occurrences of epistasis and deviations for plant height, ear height, kernel row number, ear diameter, and yield. For 300-kernel weight, Types I and II showed equal epistasis, but Type I had more occurrences of significant deviations from the full model.

Table 11. Number of crosses out of 21 in each Type which show significance at 5% for date silk and plant height. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Date silk																				
Type I	21	10	7	6									21	6	9	1				
Type II	21	4	2	2									21	0	0	0				
Type III	21	6	5	2									21	3	2	3				
Type IV	21	3	2	2									21	3	2	2				
Plant height																				
Type I	21	7	5	3	21	8	8	5	21	7	6	2	21	6	6	5	21	6	4	4
Type II	21	6	8	2	21	8	10	4	21	4	6	0	21	9	7	3	21	5	4	4
Type III	21	0	0	1	21	2	3	2	21	1	1	2	21	6	6	2	21	2	1	1
Type IV	21	9	8	5	21	11	9	5	21	4	6	0	21	8	11	4	21	3	4	0

Table 12. Number of crosses out of 21 in each Type which show significance at 1% for date silk and plant height. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Date silk																				
Type I	21	5	5	2									21	4	5	1				
Type II	21	2	1	1									21	0	0	0				
Type III	21	3	3	1									21	3	1	2				
Type IV	21	0	0	0									21	2	1	1				
Plant height																				
Type I	21	4	3	2	21	3	3	2	21	3	3	0	21	6	6	1	21	1	1	2
Type II	21	3	6	1	21	5	7	2	21	2	4	0	21	5	5	1	21	3	1	2
Type III	21	0	0	0	21	0	1	0	21	1	0	0	21	0	0	2	21	1	1	0
Type IV	21	3	5	2	21	7	9	1	21	1	3	0	21	7	8	2	21	1	1	0

Table 13. Number of crosses out of 21 in each Type which show significance at 5% for ear height and kernel row number. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Ear height																				
Type I	21	4	2	5	21	4	3	4	21	7	7	2	21	4	3	3	21	10	5	9
Type II	21	7	5	2	21	8	7	5	21	6	6	2	21	7	7	2	21	5	3	2
Type III	21	2	1	1	21	7	6	3	21	4	3	3	21	7	6	4	20	0	0	0
Type IV	21	5	9	3	21	5	4	3	21	5	8	1	21	7	9	4	21	2	5	0
Kernel row no.																				
Type I	21	4	3	3	21	0	0	0	20	4	3	2	19	3	2	5	15	4	3	1
Type II	17	3	2	1	19	5	4	3	20	3	3	2	8	2	1	2	9	5	6	1
Type III	21	2	0	2	20	2	1	1	17	2	2	0	9	2	1	2	8	3	3	2
Type IV	21	10	7	4	21	13	12	4	21	7	10	0	21	7	7	6	17	12	12	3

Table 14. Number of crosses out of 21 in each Type which show significance at 1% for ear height and kernel row number. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Ear height																				
Type I	21	3	1	2	21	3	1	3	21	2	3	0	21	3	2	1	20	3	2	5
Type II	21	2	3	1	21	4	6	1	21	3	2	1	21	5	6	1	20	2	2	2
Type III	21	1	1	1	21	5	3	2	20	2	1	0	21	5	3	2	19	0	0	0
Type IV	21	2	3	1	21	3	3	1	21	4	3	0	21	5	5	1	21	1	1	0
Kernel row no.																				
Type I	21	0	1	0	20	0	0	0	20	3	2	0	15	3	1	2	10	1	1	0
Type II	17	1	1	0	15	1	0	1	13	1	1	0	6	1	0	2	8	2	2	0
Type III	18	0	0	1	18	0	0	0	14	0	0	0	7	1	0	1	3	1	2	0
Type IV	20	5	7	1	21	9	11	1	19	5	7	0	20	6	5	1	17	8	8	1

Table 15. Number of crosses out of 21 in each Type which show significance at 5% for ear length and ear diameter. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Ear length																				
Type I	21	7	11	1	21	10	9	7	21	3	5	4	21	7	3	5	21	5	3	3
Type II	20	8	6	4	21	9	6	6	18	4	1	3	21	6	7	3	17	1	1	0
Type III	21	6	7	3	21	2	3	1	19	4	2	3	21	5	5	1	17	1	2	2
Type IV	21	8	9	6	21	6	8	3	21	9	9	4	21	2	3	2	20	4	3	2
Ear diameter																				
Type I	21	8	7	6	21	8	9	1	21	7	8	3	21	6	6	5	20	7	5	5
Type II	21	3	4	1	21	12	13	2	21	7	9	1	20	4	5	3	21	5	6	1
Type III	21	2	3	3	21	6	8	1	21	3	3	2	21	3	5	1	20	1	3	1
Type IV	21	14	13	4	21	19	18	4	21	9	9	5	21	8	9	2	21	5	7	3

Table 16. Number of crosses out of 21 in each Type which show significance at 1% for ear length and ear diameter. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Ear length																				
Type I	21	5	6	0	21	6	4	5	21	2	1	1	21	1	1	2	21	2	0	2
Type II	20	5	3	2	21	6	3	4	17	1	0	1	21	4	3	3	15	0	0	0
Type III	21	2	4	0	21	1	3	0	19	1	1	0	21	3	3	0	13	1	0	0
Type IV	21	5	4	4	21	3	3	3	21	6	7	2	21	1	2	0	19	2	2	0
Ear diameter																				
Type I	21	5	2	4	21	4	4	0	21	5	4	2	21	5	3	1	20	2	1	1
Type II	21	1	2	0	21	8	10	1	21	2	5	0	20	2	1	0	20	2	5	0
Type III	21	1	1	1	20	3	5	0	19	1	2	0	21	2	1	1	20	0	1	0
Type IV	21	11	12	3	21	13	14	3	21	6	7	3	21	4	5	0	21	4	3	1



Table 17. Number of crosses out of 21 in each Type which show significance at 5% for yield and 300-kernel weight. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Yield																				
Type I	21	7	5	4	21	2	2	3	21	3	3	3	21	6	2	6	21	1	1	1
Type II	21	2	3	1	21	5	5	1	20	2	1	4	21	4	2	3	21	2	3	0
Type III	21	2	1	0	21	0	2	0	21	5	5	1	21	3	5	4	19	1	1	1
Type IV	21	5	6	3	21	6	8	2	21	1	2	0	21	4	5	2	21	4	3	1
300-kernel wt.																				
Type I	17	8	6	3	10	1	0	1	13	4	2	5	17	1	2	2	18	2	0	4
Type II	18	6	7	0	13	2	2	0	13	0	1	0	18	2	4	0	19	2	3	1
Type III	16	7	6	2	13	2	5	0	14	4	4	1	14	4	3	3	12	2	1	1
Type IV	14	6	8	1	15	6	9	3	17	10	5	7	19	4	2	3	13	8	6	2

Table 18. Number of crosses out of 21 in each Type which show significance at 1% for yield and 300-kernel weight. Components tested against a pooled character-environment error are: (A) reduction due to fitting a and d; (B) residual after fitting m, a, and d; (C) reduction due to fitting aa, ad, and dd after m, a, and d; and (D) deviations after fitting the full model.

Character Type	Environment 1				Environment 2				Environment 3				Environment 4				Environment 5			
	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)	(A)	(B)	(C)	(D)
Yield																				
Type I	21	1	2	2	21	2	1	0	21	3	3	1	21	1	0	1	21	1	0	0
Type II	21	0	0	0	21	2	2	0	20	1	0	2	21	2	1	3	20	0	2	0
Type III	21	1	0	0	21	0	1	0	21	0	2	0	21	1	1	0	17	0	1	0
Type IV	21	3	3	2	21	4	5	0	21	1	1	0	21	3	1	1	21	2	1	0
300-kernel wt.																				
Type I	13	1	2	0	6	0	0	0	9	1	1	0	13	0	0	0	9	0	0	2
Type II	14	4	4	0	9	0	0	0	9	0	0	0	14	0	1	0	18	2	1	0
Type III	11	3	2	2	8	1	1	0	11	2	2	0	11	1	3	0	9	1	0	1
Type IV	14	4	4	1	14	2	4	2	11	8	5	3	18	2	1	2	11	6	5	1

Type III had more epistasis than Type IV for date silk. For all other characters, there were more occurrences of significant epistasis and deviations in Type IV than Type III. The differences between Types III and IV were most pronounced for plant height, kernel row number, and ear diameter. For these characters, Type IV showed epistasis in nearly one-half of the crosses.

Epistasis and significant deviations from Model 2 were found for all characters and Types in more than half of the environments. The only exception was Type II for 300-kernel weight where the incidence of significant deviations was zero in four of five environments.

Combined analyses were made over environments for each cross. The analyses were done as shown in Table 6. Counts of the occurrence of significance were then made over the 21 crosses in each Type and are presented in Tables 19 through 22. The reduction due to fitting a and d was significant in about 17 of 21 crosses for date silk in each Type. Type I had more epistasis than Type II. Type III had only slightly more than Type IV. Deviations from Model 2 were very low, the highest occurrence being in Type IV, and then only in three crosses. Environmental interactions with a and d were the same for Types I and II and Type IV showed more than Type III. Occurrences of environmental interaction with epistasis and deviations from Model 2 were of low incidence for all Types, with slightly more total occurrences of environmental interaction with deviations than epistasis.

Plant and ear height both had 21 of 21 crosses significant for the reduction due to a and d in all Types for the combined analyses. Epistasis occurred in about the same frequency for both characters, with Types I and

II approximately equal and Type IV showing much more epistasis than Type III. Deviations from Model 2 were about equal between Types I and II for both characters. Plant height deviations were more for Type III than IV and ear height deviations were equal. Environmental interactions with a and d were equal between Types I and II for plant height, but Type II had relatively more occurrences for ear height. For both characters, Type IV had more interaction with a and d than Type III. Interactions with epistasis and deviations were low for plant height; however, for ear height Types I and II had a relatively higher frequency of significance, especially Type I.

Kernel row number had 21 of 21 cases of significance for the reduction in sums of squares due to a and d, except for Type II. The occurrence of epistasis in Types II and IV was twice as much as in Types I and III. Deviations from Model 2 and interactions of environments with epistasis and deviations were all of similar low frequency. Types I and II had about equal incidences of environmental interaction with a and d, while Type III had only one-fifth as many crosses significant as Type IV.

Ear length and diameter had all crosses significant for the reduction due to a and d. Epistasis occurred in nearly the same frequency for both characters. Type I showed less epistasis than Type II and Type III showed less than Type IV. Type IV epistasis for ear diameter was particularly high with 18 of 21 crosses showing significance. Deviations from Model 2 were about equal for both characters for Types I and II. Type IV showed a relatively high frequency of deviations (7 of 21) for ear length, while for ear diameter the occurrence of significant deviations for Types III and IV were equally low. Environmental interactions with a and d were much

more frequent for ear length than ear diameter. Ear length interactions were equal for Types I, II, and III, and slightly lower for Type IV. Type IV had more environmental interactions with a and d than Type III, and Types I and II were about equal. Environmental interactions with epistasis and deviations were low for both characters, except Type I inbreds' interactions with deviations. There were relatively more interactions with epistasis and deviations for Type IV than Type III.

All crosses were significant for the reduction due to a and d in the combined analyses for yield. Type II crosses had five times as much epistasis as those of Type I, with the former's frequency at about one-half. Epistasis was found about one-third of the time for Type III and IV. Type I had the highest deviations from Model 2, with other Types all being quite low. Environment x a and d interactions were the highest of any character, averaging significance in over two-thirds of the crosses in a Type. Types I and II were about the same and Type IV had five more instances of interaction than Type III. Epistatic and deviations interactions with environments were near zero for Types II and III. They were equal for Type I and there was more epistatic interaction than deviation interaction in Type IV.

300-kernel weight had the fewest instances of a significant reduction due to a and d of any of the characters studied. Types II and III showed slightly more cases of significance than Types I and IV respectively. Types I and II contained equal occurrences of epistasis and these were half the frequency of epistasis in Types III and IV. Significant deviations from Model 2 occurred in about one-fifth of the crosses in Types I, III, and IV and only one in Type II. Environmental interaction with a and d was in a ratio of about two to one for Types II and I, and Types IV and III,

Table 19. Number of crosses out of 21 in each Type combined over environments which show significance at 5% for date silk, plant height, ear height, and kernel row number. Main effects are tested against their respective interactions with environments; environmental interactions are tested against a pooled error for each character.

Source	df	Date silk				Plant height				Ear height				Kernel row no.			
		Type				Type				Type				Type			
		I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Environments	4 (1) <sup>†</sup>																
Generations	8	21	21	20	21	21	21	21	21	21	21	21	21	21	20	21	21
a, d	2	16	17	18	16	21	21	21	21	21	21	21	21	21	18	21	21
Residual	6	7	2	7	3	12	15	12	15	9	12	10	14	7	9	6	17
Epistasis	3	5	1	5	3	11	13	6	15	11	12	9	15	6	12	8	17
Deviations	3	1	1	1	3	4	6	7	3	3	3	6	6	0	2	3	2
Env. x Gen.	32 (8)	6	3	3	4	7	10	3	9	10	10	7	8	6	3	1	7
Env. x a, d	8 (2)	5	4	0	3	10	9	11	15	9	14	12	14	8	6	2	10
Env. x Res.	24 (6)	3	1	4	0	3	5	2	1	6	3	0	1	1	0	1	3
Env. x Epi.	12 (3)	3	0	1	1	1	2	0	0	4	2	1	1	1	0	0	2
Env. x Dev.	12 (3)	2	1	3	1	2	3	2	1	8	5	1	2	0	3	2	3
Pooled Dev.	15 (6)	6	2	4	3	9	5	3	2	10	7	4	3	2	4	4	8

<sup>†</sup> Degrees freedom for date silk are shown in parentheses.

Table 20. Number of crosses out of 21 in each Type combined over environments which show significance at 1% for date silk, plant height, ear height, and kernel row number. Main effects are tested against their respective interactions with environments; environmental interactions are tested against a pooled error for each character.

Source	df	Date silk				Plant height				Ear height				Kernel row no.			
		Type				Type				Type				Type			
		I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Environments	4 (1) <sup>†</sup>																
Generations	8	21	19	18	21	21	21	21	21	21	21	21	21	21	17	21	21
a, d	2	9	6	10	2	21	21	21	21	21	21	21	21	21	16	21	21
Residual	6	0	0	1	2	9	11	5	12	7	8	6	9	2	8	2	12
Epistasis	3	1	0	1	0	9	12	2	11	5	9	6	13	3	7	5	16
Deviations	3	1	0	0	1	1	1	2	1	1	0	0	2	0	1	2	1
Env. x Gen.	32 (8)	1	1	1	1	4	6	2	5	7	6	3	3	3	1	1	2
Env. x a, d	8 (2)	0	2	0	1	5	5	6	12	4	8	8	8	3	3	1	4
Env. x Res.	24 (6)	1	0	3	0	1	1	0	0	4	1	0	0	1	0	0	1
Env. x Epi.	12 (3)	0	0	1	0	0	2	0	0	1	1	0	0	1	0	0	0
Env. x Dev.	12 (3)	1	0	2	0	2	2	0	0	6	1	0	0	0	0	0	1
Pooled Dev.	15 (6)	2	1	3	0	5	5	0	1	8	4	2	1	1	1	1	3

<sup>†</sup> Degrees freedom for date silk are shown in parentheses.

Table 21. Number of crosses out of 21 in each Type combined over environments which show significance at 5% for ear length, ear diameter, yield, and 300-kernel weight. Main effects are tested against their respective interactions with environments; environmental interactions are tested against a pooled error for each character.

Source	df	Ear length				Ear diameter				Yield				300-Kernel wt.			
		Type				Type				Type				Type			
		I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Environments	4																
Generations	8	21	21	21	21	21	21	21	21	21	21	21	21	17	19	19	19
a, d	2	21	21	21	21	21	21	21	21	21	21	21	21	16	19	16	14
Residual	6	11	10	10	11	12	15	10	17	7	8	5	9	7	6	13	15
Epistasis	3	6	11	9	13	8	11	10	18	2	10	6	7	5	6	13	13
Deviations	3	4	3	2	7	4	5	2	3	5	2	1	3	6	1	4	5
Env. x Gen.	32	12	7	7	9	9	5	6	6	11	8	5	13	4	7	6	15
Env. x a, d	8	11	11	11	8	6	5	4	7	16	14	13	18	4	8	10	17
Env. x Res.	24	4	2	1	5	5	2	1	4	4	2	0	3	1	2	2	2
Env. x Epi.	12	2	1	1	4	3	3	1	2	3	0	0	5	2	1	0	2
Env. x Dev.	12	5	4	1	3	5	0	2	4	3	1	1	2	1	0	2	4
Pooled Dev.	15	9	7	2	5	10	2	3	7	8	3	1	3	4	2	2	6



Table 22. Number of crosses out of 21 in each Type combined over environments which show significance at 1% for ear length, ear diameter, yield, and 300-kernel weight. Main effects are tested against their respective interactions with environments; environmental interactions are tested against a pooled error for each character.

Source	df	Ear length				Ear diameter				Yield				300-Kernel wt.			
		Type				Type				Type				Type			
		I	II	III	IV	I	II	III	IV	I	II	III	IV	I	II	III	IV
Environments	4																
Generations	8	21	21	21	21	21	21	21	21	21	21	21	21	17	18	17	15
a, d	2	21	21	21	21	21	21	21	21	21	21	21	21	14	15	12	11
Residual	6	6	6	6	9	7	9	8	14	4	5	2	3	4	3	6	8
Epistasis	3	4	4	5	8	6	7	8	12	1	5	2	3	1	3	6	7
Deviations	3	2	2	0	2	3	3	0	2	3	0	1	1	1	0	1	3
Env. x Gen.	32	6	3	3	6	6	2	1	3	7	4	2	11	1	5	3	10
Env. x a, d	8	8	5	8	5	3	4	1	2	12	11	10	15	3	6	7	14
Env. x Res.	24	1	1	1	2	2	0	1	1	3	0	0	2	0	0	0	0
Env. x Epi.	12	1	0	0	1	1	0	0	0	0	0	0	2	0	1	0	0
Env. x Dev.	12	3	1	0	1	1	0	1	2	1	0	0	1	1	0	0	1
Pooled Dev.	15	6	2	2	3	5	0	0	5	3	1	0	3	3	0	0	5

respectively. The incidence of significant interactions was much greater in Types III and IV. The remaining epistatic and deviations interactions with environments were as low as for any character.

Pooled deviations, obtained by pooling sums of squares and degrees of freedom for deviations and environments x deviations, are shown, but no generalization could be made regarding a relationship between the three sources, beyond the usual result of partitioning a source of variation.

Tables 23 through 30 contain the results of pooling the combined analyses for each character over Types. For date silk, all Types were significant for a and d, epistasis, and pooled deviations. All Types but Type III were significant for deviations from Model 2 and the interaction of a and d with environments. Type III had a significant interaction of deviations with environments.

Plant and ear height showed significance for all Types for the following sources: a and d, epistasis, deviations from Model 2, environment x a and d, and pooled deviations. For both characters, Type I was significant for environment x deviations; and for ear height, Type II was significant.

All Types, for kernel row number, were significant for a and d, epistasis, deviations, pooled deviations, and the environment x a and d interaction. None of the other interactions were significant.

Ear length and diameter were significant for all Types for a and d, epistasis, and the interaction of a and d with environments. Ear length showed significance for all Types for deviations from Model 2. Ear length also had significance in Types I, II, and IV for pooled deviations; Types I and II for environments x deviations; and Type I for environments x epistasis. Ear diameter was significant in Types I, II, and III for

deviations and environments x epistasis, and in Types II and IV for environments x deviations and pooled deviations.

The combined and pooled analyses for yield showed all Types significant for a and d, epistasis, and environments x a and d. Types I and IV exhibited significant deviations from Model 2 and significant pooled deviations. Type IV displayed presence of environments x epistasis interaction and Type I showed significant interaction of environments and deviations.

300-kernel weight was significant for a and d, and epistasis for all four Types. Types I, III, and IV had significant deviations from Model 2. Types I, II, and IV were significant for environments x a and d; Types I and IV for pooled deviations; Type II for environments x epistasis; and Type IV for environments by deviations.

Significance in itself told only part of the story; the rest was contained in the magnitudes of the mean squares. The mean squares for a and d were larger for Type I than Type II for all characters but 300-kernel weight. For epistasis, the mean squares for Type II were greater than those for Type I, in all characters but date silk. Deviations from Model 2 were higher for all characters in Type I. The interactions with environments were nearly equal. Date silk, plant height, ear height, ear diameter, and 300-kernel weight had larger environment x a and d mean squares for Type II than Type I. Significance among the remaining interactions was too small to make such comparisons.

The comparison between Types III and IV found the mean square for reduction due to a and d to be more for Type IV than Type III in all characters but date silk. Likewise, more epistasis was present in Type IV than Type III for all but date silk. Ear height was the only character in which

Table 23. Analysis of variance by Types for date silk combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	21	219.6233**	287.5315**	286.0559**	262.8945**
Generations	168	21.3530**	16.3380**	16.8380**	16.1488**
a, d	42	73.7574**	60.2530**	60.6380**	58.9906**
Residual	126	3.8849**	1.6997**	2.2380**	1.8681**
Epistasis	63	5.2714**	1.6577*	2.7727**	1.9438**
Deviations	63	2.4984**	1.7417*	1.7034	1.7924*
Env. x Gen.	168	1.3876*	1.2583	1.1690	1.2147
Env. x a, d	42	1.7298*	1.9092**	0.8175	2.1491**
Env. x Res.	126	1.2736	1.0413	1.2861	0.9032
Env. x Epi.	63	1.3430	1.0250	1.0494	0.8029
Env. x Dev.	63	1.2041	1.0577	1.5228*	1.0036
Pooled Dev.	126	1.8513**	1.3997*	1.6131**	1.3980*
Pooled error	23541	1.1212	1.1212	1.1212	1.1212

\* indicates significance at 5%; \*\* at 1%.

Table 24. Analysis of variance by Types for plant height combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	1819.8333**	1453.9031**	1374.1965**	1234.4143**
Generations	168	2117.0647**	1933.4058**	1479.7451**	2531.6108**
a, d	42	8101.0000**	7326.5117**	5730.7227**	9677.5430**
Residual	126	122.4134**	135.6976**	62.7453**	149.6250**
Epistasis	63	164.1858**	203.8372**	73.6153**	244.6572**
Deviations	63	80.6411**	67.5577**	51.8754**	54.5929**
Env. x Gen.	672	41.3454**	37.8420**	35.1044**	41.6833**
Env. x a,d	168	57.0627**	59.9484**	66.4449**	79.1702**
Env. x Res.	504	36.1063**	30.4733	24.6576	29.1877
Env. x Epi.	252	31.8118	29.9994	23.2014	27.8974
Env. x Dev.	252	40.4009**	30.9471	26.1138	30.4778
Pooled Dev.	315	48.4489**	38.2692**	31.2661	35.3009*
Pooled error	59115	29.7813	29.7813	29.7813	29.7813

\* indicates significance at 5%; \*\* at 1%.

Table 25. Analysis of variance by Types for ear height combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	1139.9138**	596.8303**	630.6921**	721.7200**
Generations	168	873.5010**	762.8135**	645.4363**	966.6118**
a, d	42	3307.8750**	2843.7004**	2434.6846**	3628.6338**
Residual	126	62.0421**	69.1859**	49.0214**	79.2722**
Epistasis	63	78.5700**	104.0700**	55.8061**	125.2795**
Deviations	63	45.5143**	34.3019**	42.2367**	33.2649**
Env. x Gen.	672	26.8718**	25.3966**	23.6691**	23.9176**
Env. x a, d	168	34.4933**	40.6430**	41.5760**	43.1851**
Env. x Res.	504	24.3313**	20.3145*	17.7002	17.4951
Env. x Epi.	252	19.3978	19.0053	16.8376	15.6561
Env. x Dev.	252	29.2650**	21.6237*	18.5628	19.3342
Pooled Dev.	315	32.5148**	24.1594**	23.2976**	22.1203**
Pooled error	59052	17.8279	17.8279	17.8279	17.8279

\* indicates significance at 5%; \*\* at 1%.

Table 26. Analysis of variance by Types for kernel row number combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	5.0881**	4.3321**	7.9471**	4.8270**
Generations	168	4.8920**	2.3262**	2.3524**	7.6729**
a, d	42	17.8125**	6.9246**	7.7981**	24.3916**
Residual	126	0.5852**	0.7934**	0.5372**	2.1000**
Epistasis	63	0.6751**	1.1359**	0.6486**	3.6115**
Deviations	63	0.4952**	0.4509**	0.4258*	0.5885**
Env. x Gen.	672	0.3284**	0.3010*	0.2735	0.3589**
Env. x a, d	168	0.4543**	0.4449**	0.3317*	0.5176**
Env. x Res.	504	0.2865	0.2530	0.2541	0.3060*
Env. x Epi.	252	0.2744	0.2179	0.2135	0.2700
Env. x Dev.	252	0.2985	0.2881	0.2946	0.3421**
Pooled Dev.	315	0.3378**	0.3207*	0.3209*	0.3914**
Pooled error	55545	0.2722	0.2722	0.2722	0.2722

\* indicates significance at 5%; \*\* at 1%.

Table 27. Analysis of variance by Types for ear length combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	16.7757**	22.6809**	24.4065**	16.7934**
Generations	168	23.6620**	12.0263**	11.3582**	27.2409**
a, d	42	88.5871**	42.6165**	40.5118**	99.8454**
Residual	126	2.0204**	1.8295**	1.6404**	3.0395**
Epistasis	63	2.3645**	2.3900**	2.3716**	4.4187**
Deviations	63	1.6763**	1.2690**	0.9091**	1.6603**
Env. x Gen.	672	0.9389**	0.8312**	0.7508**	0.8303**
Env. x a, d	168	1.4194**	1.2405**	1.3370**	1.2786**
Env. x Res.	504	0.7788**	0.6948*	0.5554	0.6809
Env. x Epi.	252	0.7400*	0.6195	0.5471	0.7101
Env. x Dev.	252	0.8175**	0.7701**	0.5637	0.6516
Pooled Dev.	315	0.9893**	0.8699**	0.6328	0.8534**
Pooled error	55545	0.6185	0.6185	0.6185	0.6185

\* indicates significance at 5%; \*\* at 1%.



Table 28. Analysis of variance by Types for ear diameter combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	0.5223**	0.4268**	0.6130**	0.4293**
Generations	168	0.4002**	0.3462**	0.2579**	0.5224**
a, d	42	1.4465**	1.2265**	0.9288**	1.8253**
Residual	126	0.0515**	0.0528**	0.0342**	0.0881**
Epistasis	63	0.0679**	0.0825**	0.0544**	0.1449**
Deviations	63	0.0350**	0.0231**	0.0141	0.0313**
Env. x Gen.	672	0.0169**	0.0152**	0.0141*	0.0163**
Env. x a, d	168	0.0195**	0.0199**	0.0152*	0.0200**
Env. x Res.	504	0.0160**	0.0136	0.0137	0.0151**
Env. x Epi.	252	0.0161**	0.0162**	0.0132	0.0146*
Env. x Dev.	252	0.0159**	0.0110	0.0142	0.0157**
Pooled Dev.	315	0.0197**	0.0134	0.0142	0.0188**
Pooled error	55545	0.0124	0.0124	0.0124	0.0124

\* indicates significance at 5%; \*\* at 1%.

Table 29. Analysis of variance by Types for yield combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	5482.4922**	6376.5078**	7412.5234**	5136.8984**
Generations	168	5659.7422**	5611.4297**	4132.8672**	8042.1328**
a, d	42	21669.1641**	21425.1758**	15697.3125**	30527.7344**
Residual	126	323.2766**	340.1960**	278.0522**	546.9397**
Epistasis	63	311.8948**	493.7100**	409.1492**	793.2117**
Deviations	63	334.6584**	186.6824	146.9556	300.6682**
Env. x Gen.	672	216.0024**	195.8616**	177.8697**	251.8168**
Env. x a, d	168	410.2683**	336.3499**	322.2522**	524.5137**
Env. x Res.	504	151.2473	149.0322	129.7420	160.9183**
Env. x Epi.	252	133.2122	146.7955	132.4308	177.4202**
Env. x Dev.	252	169.2824*	151.2690	127.0533	144.4164
Pooled Dev.	315	202.3577**	158.3517	131.0338	175.6669**
Pooled error	55377	139.1366	139.1366	139.1366	139.1366

\* indicates significance at 5%; \*\* at 1%.

Table 30. Analysis of variance by Types for 300-kernel weight combined over environments and pooled over 21 crosses in each Type. Main effects are tested against their respective interactions with environments; all other sources are tested against the pooled error.

Source	df	Mean squares			
		Type I	Type II	Type III	Type IV
Environments	84	529.1880**	386.6453**	468.4973**	579.5288**
Generations	168	164.8110**	194.7456**	159.6088**	344.3499**
a, d	42	536.5276**	648.8296**	467.8257**	1049.8308**
Residual	126	40.9049**	43.3838**	56.8693**	109.1899**
Epistasis	63	38.6286**	66.6880**	86.0802**	154.7571**
Deviations	63	43.1813**	20.0796	27.6584**	63.6226**
Env. x Gen.	672	22.4821**	26.1369**	23.5471**	33.4443**
Env. x a, d	168	32.0667**	41.5543**	42.9255	65.2511**
Env. x Res.	504	19.2872	20.9978	17.0877	22.8421**
Env. x Epi.	252	18.3336	22.6666*	16.7698	22.3183
Env. x Dev.	252	20.2408	19.3289	17.4056	23.3658*
Pooled Dev.	315	24.8289**	19.4790	19.4562	31.4172**
Pooled error	55167	19.5827	19.5827	19.5827	19.5827

\* indicates significance at 5%; \*\* at 1%.

Type III had a higher deviation mean square than Type IV; and ear length was the only character which had a larger mean square for environments x a and d in Type III than Type IV. With the exception of date silk, the interactions with epistasis and deviations were generally larger for Type IV than Type III.

In general, removing the environmental and Model 1 sums of squares largely accounted for the variability present. A much smaller amount was removed by epistasis and deviations from Model 2 and the interaction terms removed much less variation than did epistasis and deviations.

#### Tests of Individual Effects

The tests for presence of individual effects were computed as the usual t-test, with standard errors obtained as outlined in the statistical procedures section. The standard errors for the various pooled and combined effects are given in Tables 47, 54, and 75, following their respective effects. Errors for date silk were calculated based on two environments versus five for the other traits. Standard errors for the differences were calculated by multiplying the appropriate error by  $\sqrt{2}$ .

Effects and their standard errors are shown rounded to two decimal places; however, the tests of significance were carried out before rounding, using four places beyond the decimal. In several instances this has caused apparent discrepancies, but the significance levels as shown are correct. "Hats" are used in the text to denote estimates, while in the tables the effects are denoted by the corresponding parameters.

No problems occurred when effects combined over environments were considered; however, pooled effects within a Type had certain complica-

tions. Due to the structure of the generation mean analysis, the signs on the coefficients for  $a$  and  $ad$  were positive for  $P_1$ ,  $BC_1$ , and  $BS_1$  where the effects occurred. If the  $P_1$  and  $P_2$  were reversed, the signs on the estimates of the effects would also reverse. The first inbred parent was used six times as  $P_1$ , the second inbred was used five times, the third inbred was used four times, and so on. Some cancellation of effects was certain to have occurred for the inbreds which were both  $P_1$  or  $P_2$ , depending on the particular cross. Therefore, it must be remembered that in looking at  $\hat{a}$  and  $\hat{ad}$ , the value tabled was the net effect, including some unknown degree of cancellation due to which parent was designated  $P_1$ .

Effects were pooled over crosses within a Type in each environment in Tables 31, 33, 35, 37, 39, 41, 43, and 45. The differences between Types I and II, and Types III and IV for each environment are in Tables 32, 34, 36, 38, 40, 42, 44, and 46. Effects from both models are presented. However, Hayman (1960) pointed out the fallacy of looking at  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$  of Model 2 in the presence of significant epistasis. Therefore, consideration should be given only to  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$  of Model 1 and  $\hat{aa}$ ,  $\hat{ad}$ , and  $\hat{dd}$  of Model 2 as in the second case of Hayman (1960), where epistasis was significant but of lesser importance than  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$ . When the magnitude of an effect was considered, the coefficient of the effect had to be kept in mind, e.g.,  $\hat{dd}$  cannot occur with a coefficient larger than one-fourth.

With date silk,  $\hat{m}$  and  $\hat{d}$  were significant for all Types in both environments. The  $\hat{a}$  and  $\hat{aa}$  effects were present for Types III and IV in both environments. Type III also had a significant  $\hat{dd}$  effect in both environments. Significant differences between  $\hat{m}$  and  $\hat{a}$  were noted in both environments for both comparisons (Type I vs. Type II and Type III vs. Type IV).

Only the second comparison (Type III vs. Type IV) was significant for  $\hat{d}$  in both environments (Tables 31 and 32).

The  $\hat{m}$  and  $\hat{d}$  effects were significant for all Types in all environments for plant height and  $\hat{a}$  was significant in more than half of the environments. The  $\hat{dd}$  effect was present in all environments for Types II and IV and in four of five environments for Type I. Significant differences for both comparisons were present in all environments for  $\hat{m}$  and in nearly all environments for  $\hat{a}$ . No significant differences occurred for  $\hat{d}$  in the first comparison, but significant differences did occur for  $\hat{d}$  and  $\hat{dd}$  in the second comparison in most environments (Tables 33 and 34).

Effects significant in all Types and environments for ear height were  $\hat{m}$  and  $\hat{d}$ . The  $\hat{a}$  and  $\hat{dd}$  effects were significant in more than half the environments for all Types. Type I had a significant  $\hat{aa}$  effect in more than half the environments, as did Type II for  $\hat{ad}$ . The estimate of  $m$  was significantly different in both comparisons in all environments. The first comparison was significant for  $\hat{a}$  in all environments; the second comparison for  $\hat{a}$  in three of five environments and for  $\hat{dd}$  in all environments (Tables 35 and 36).

Kernel row number had  $\hat{m}$  and  $\hat{d}$  significant for all Types in all environments and  $\hat{a}$  for all Types in more than half the environments. Type IV showed significant  $\hat{aa}$  and  $\hat{dd}$  in most environments. Comparisons between Types revealed significant differences for  $\hat{m}$  and  $\hat{a}$  in all environments. The second comparison was significant in at least half the environments for  $\hat{d}$  and  $\hat{aa}$  (Tables 37 and 38).

Ear length showed  $\hat{m}$  and  $\hat{d}$  to be significant in all instances. Most of the environments had  $\hat{a}$  significant for all Types, while  $\hat{aa}$  was present only

Table 31. Significance of individual effects by Types within environments for date silk.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	29.68**	0.25	-7.85**	29.93**	0.43	-8.60**	-0.75	0.23	-0.97
Type II	26.74**	-0.52*	-7.04**	26.79**	-0.75*	-7.59**	-0.64	-0.32	0.87
Type III	26.44**	-0.45**	-5.99**	26.24**	-1.27**	-6.87**	-1.23**	-1.10**	4.67**
Type IV	29.61**	0.97**	-8.58**	29.60**	0.69*	-9.83**	-1.56**	-0.37	3.41**
Env. 2									
Type I									
Type II									
Type III									
Type IV									
Env. 3									
Type I									
Type II									
Type III									
Type IV									
Env. 4									
Type I	36.85**	0.24	-6.35**	36.99**	0.64*	-6.98**	-0.68	0.53	-0.04
Type II	34.77**	-0.24	-6.41**	34.65**	-0.60*	-6.98**	-0.78	-0.47	2.95**
Type III	34.44**	-0.43**	-5.61**	34.25**	-0.11	-6.61**	-1.36**	0.42	4.77**
Type IV	37.53**	1.56**	-6.50**	37.56**	1.84**	-7.38**	-1.07*	0.38	1.92
Env. 5									
Type I									
Type II									
Type III									
Type IV									

\* indicates significance at 5%; \*\* at 1%.

Table 32. Significance of differences between individual effects of Type I and II, and Types III and IV within environments for date silk.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	2.94**	0.77**	-0.81*	3.15**	1.18**	-1.01	-0.11	0.55	-1.84
III-IV	-3.18**	-1.42**	2.59**	-3.37**	-1.96**	2.96**	0.33	-0.73	1.25
Env. 2									
I-II									
III-IV									
Env. 3									
I-II									
III-IV									
Env. 4									
I-II	2.08**	0.48**	0.06	2.35**	1.23**	-0.00	0.11	1.00*	-2.99*
III-IV	-3.08**	-1.99**	0.88*	-3.31**	-1.96**	0.77	-0.29	0.04	2.85
Env. 5									
I-II									
III-IV									

\* indicates significance at 5%; \*\* at 1%.



Table 33. Significance of individual effects by Types within environments for plant height.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	198.66**	2.05**	59.68**	199.06**	-0.61	65.42**	7.35**	-3.55*	-19.72**
Type II	184.72**	-6.68**	59.85**	186.03**	-9.61**	59.27**	0.20	-3.90*	-13.97**
Type III	180.24**	1.77**	56.08**	180.23**	2.00	59.70**	4.46*	0.31	-9.31
Type IV	193.37**	-3.05**	68.33**	195.30**	-2.22	69.53**	2.81	1.11	-25.95**
Env. 2									
Type I	212.91**	0.03	64.97**	213.89**	0.77	65.39**	1.19	0.98	-12.61**
Type II	192.56**	-6.61**	63.58**	194.94**	-8.23**	61.93**	-0.38	-2.16	-23.85**
Type III	188.67**	1.63**	57.48**	188.93**	2.61*	58.71**	1.70	1.29	-6.24
Type IV	201.69**	-3.92**	73.44**	204.45**	-0.00	70.49**	-1.72	5.22**	-24.91**
Env. 3									
Type I	192.35**	2.34**	52.37**	194.31**	0.42	50.29**	-1.20	-2.56	-17.73**
Type II	179.14**	-3.80**	49.80**	181.03**	-5.27**	49.46**	0.89	-1.97	-21.38**
Type III	171.84**	2.83**	43.73**	171.35**	3.15**	43.97**	-0.04	0.43	5.09
Type IV	188.05**	-6.71**	55.87**	189.70**	-3.56**	57.60**	3.29	4.21**	-24.13**
Env. 4									
Type I	217.14**	2.32**	65.39**	218.53**	1.20	66.14**	1.89	-1.50	-18.44**
Type II	200.80**	-7.77**	64.19**	202.63**	-10.51**	62.29**	-1.08	-3.64*	-16.58**
Type III	189.32**	-0.67	51.83**	188.81**	-0.98	53.27**	1.42	-0.41	2.29
Type IV	207.86**	-1.07	73.82**	210.44**	-1.44	70.79**	-1.94	-0.49	-22.59**
Env. 5									
Type I	180.99**	3.37**	50.85**	181.85**	0.07	52.83**	3.04	-4.40	-15.35
Type II	167.39**	-3.65**	54.92**	170.08**	-4.37**	57.58**	5.15	-0.97	-38.73**
Type III	160.25**	-2.09*	46.70**	160.27**	-1.58	52.53**	7.19*	0.68	-15.46
Type IV	176.37**	0.94	56.93**	178.96**	1.82	57.18**	2.10	1.17	-31.23**

\* indicates significance at 5%; \*\* at 1%.

Table 34. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for plant height.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	13.94**	8.73**	-0.17	13.03**	9.00**	6.15*	7.16*	0.36	-5.75
III-IV	-13.13**	4.82**	-12.25**	-15.07**	4.22*	-9.82**	1.64	-0.80	16.64*
Env. 2									
I-II	20.36**	6.63**	1.40	18.95**	8.99**	3.46	1.57	3.15	11.24
III-IV	-13.02**	5.55**	-15.96**	-15.52**	2.61	-11.77**	3.42	-3.93	18.67**
Env. 3									
I-II	13.21**	6.14**	2.57	13.28**	5.69**	0.83	-2.09	-0.59	3.65
III-IV	-16.21**	9.54**	-12.13**	-18.35**	6.71**	-13.63**	-3.33	-3.77	29.22**
Env. 4									
I-II	16.33**	10.10**	1.19	15.90**	11.71**	3.85	2.97	2.14	-1.86
III-IV	-18.54**	0.40	-21.99**	-21.63**	0.47	-17.51**	3.37	0.09	24.88**
Env. 5									
I-II	13.59**	7.02**	-4.07	11.77**	4.44	-4.75	-2.11	-3.43	23.38*
III-IV	-16.12**	-3.03*	-10.23**	-18.69**	-2.40	-4.65	5.09	-0.50	15.77

\* indicates significance at 5%; \*\* at 1%.

Table 35. Significance of individual effects by Types within environments for ear height.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	100.79**	0.51	34.42**	100.79**	-1.18	38.45**	4.97**	-2.26	-10.58**
Type II	75.31**	-5.33**	33.30**	76.26**	-7.44**	33.43**	0.82	-2.82*	-11.64**
Type III	73.78**	1.88**	30.48**	72.92**	1.39	32.39**	1.75	-0.65	5.21
Type IV	85.97**	1.87**	40.42**	87.36**	1.90	41.45**	2.22	0.03	-19.06**
Env. 2									
Type I	111.03**	1.38**	37.63**	111.23**	1.97	40.01**	3.08	0.79	-8.59*
Type II	81.49**	-5.56**	40.03**	83.33**	-6.16**	35.85**	-3.87*	-0.80	-10.76**
Type III	81.37**	2.43**	35.97**	81.55**	3.40**	37.15**	1.58	1.29	-5.32
Type IV	89.86**	0.22	40.90**	91.70**	2.05	40.05**	0.23	2.44	-19.48**
Env. 3									
Type I	99.38**	1.48**	26.54**	100.47**	1.71	28.11**	2.69	0.30	-16.97**
Type II	75.17**	-5.25**	26.38**	76.19**	-7.25**	26.07**	0.33	-2.67*	-11.24**
Type III	72.66**	4.68**	22.84**	71.81**	5.52**	24.24**	1.13	1.12	6.43
Type IV	84.15**	-0.24	29.55**	85.42**	0.59	28.58**	-0.31	1.10	-12.52**
Env. 4									
Type I	112.26**	1.21*	35.14**	112.66**	-0.01	39.80**	6.02**	-1.64	-16.86**
Type II	86.13**	-4.43**	39.73**	87.53**	-6.74**	37.34**	-1.97	-3.08*	-10.24*
Type III	81.18**	0.36	30.46**	80.23**	1.68	31.27**	0.33	1.76	9.13*
Type IV	93.26**	3.70**	43.45**	94.83**	5.09**	40.18**	-2.93	1.85	-10.12*
Env. 5									
Type I	83.47**	0.58	25.87**	83.76**	-3.26*	29.59**	4.79*	-5.12**	-13.14*
Type II	64.12**	-2.84**	28.14**	65.41**	-2.73	28.22**	0.99	0.13	-15.44**
Type III	60.83**	1.35	24.13**	60.96**	0.08	26.63**	3.16	-1.69	-8.05
Type IV	69.25**	3.07**	30.29**	71.23**	2.74	30.91**	2.14	-0.44	-25.07**

\* indicates significance at 5%; \*\* at 1%.

Table 36. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for ear height.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	25.48**	5.84**	1.11	24.53**	6.26**	5.02*	4.15	0.56	1.06
III-IV	-12.20**	0.01	-9.95**	-14.44**	-0.50	-9.06**	-0.47	-0.69	24.27**
Env. 2									
I-II	29.54**	6.94**	-2.40	27.91**	8.13**	4.16	6.95**	1.59	2.17
III-IV	-8.50**	2.22**	-4.93**	-10.14**	1.35	-2.90	1.36	-1.16	14.15*
Env. 3									
I-II	24.21**	6.73**	0.16	24.28**	8.96**	2.05	2.37	2.97	-5.73
III-IV	-11.48**	4.92**	-6.70**	-13.61**	4.94**	-4.33*	1.44	0.02	18.95**
Env. 4									
I-II	26.13**	5.65**	-4.59**	25.14**	6.73**	2.46	7.99**	1.44	-6.62
III-IV	-12.07**	-3.34**	-12.99**	-14.60**	-3.41*	-8.91**	3.26	-0.09	19.26**
Env. 5									
I-II	19.35**	3.41**	-2.27	18.36**	-0.53	1.37	3.80	-5.25*	2.30
III-IV	-8.42**	-1.72	-6.16**	-10.27**	-2.66	-4.28	1.02	-1.25	17.02*

\* indicates significance at 5%; \*\* at 1%.

Table 37. Significance of individual effects by Types within environments for kernel row number.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	15.57**	0.04	1.97**	15.60**	0.01	2.00**	0.06	-0.04	-0.45
Type II	15.77**	-0.23**	1.73**	15.93**	-0.48**	1.49**	-0.19	-0.34*	-1.25*
Type III	16.24**	0.13*	2.00**	16.35**	0.23	1.88**	-0.08	0.14	-0.91
Type IV	15.29**	0.59**	2.56**	15.55**	0.78**	2.12**	-0.36	0.25	-1.92**
Env. 2									
Type I	15.30**	0.20**	2.12**	15.42**	0.17	2.14**	0.12	-0.04	-1.48**
Type II	15.54**	-0.23**	1.69**	15.69**	-0.32*	1.40**	-0.25	-0.12	-1.03
Type III	16.10**	0.20**	2.13**	16.20**	0.32*	2.24**	0.21	0.16	-1.44**
Type IV	15.12**	0.58**	3.45**	15.54**	0.83**	2.46**	-0.93**	0.33	-2.36**
Env. 3									
Type I	15.31**	-0.00	1.82**	15.44**	-0.03	1.63**	-0.13	-0.04	-1.13*
Type II	15.82**	-0.30**	1.84**	16.01**	-0.55**	1.35**	-0.47*	-0.33	-0.91
Type III	16.17**	0.23**	1.92**	16.26**	0.22	1.75**	-0.15	-0.01	-0.61
Type IV	15.18**	0.59**	2.52**	15.52**	0.72**	1.62**	-0.87**	0.19	-1.70**
Env. 4									
Type I	15.78**	0.25**	1.77**	15.89**	0.11	1.52**	-0.23	-0.19	-0.72
Type II	15.51**	-0.18**	0.68**	15.64**	-0.28	0.31	-0.37	-0.13	-0.63
Type III	16.09**	0.01	1.57**	16.24**	0.01	1.47**	-0.01	0.01	-1.56**
Type IV	15.43**	0.63**	1.94**	15.67**	0.82	1.71**	-0.13	0.25	-2.18**
Env. 5									
Type I	13.83**	0.27**	0.88**	13.93**	0.08	0.62**	-0.24	-0.26	-0.56
Type II	14.19**	-0.31**	0.73**	14.36**	-0.62**	0.37	-0.33	-0.41*	-1.11*
Type III	14.04**	0.06	0.94**	14.08**	-0.13	0.98**	0.08	-0.26	-0.60
Type IV	13.63**	0.85**	1.56**	13.95**	0.99**	0.76**	-0.76**	0.19	-1.75**

\* indicates significance at 5%; \*\* at 1%.

Table 38. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for kernel row number.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	-0.20**	0.27**	0.24	-0.33**	0.49**	0.51	0.24	0.30	0.79
III-IV	0.95**	-0.46**	-0.56**	0.80**	-0.55**	-0.25	0.27	-0.11	1.01
Env. 2									
I-II	-0.24**	0.43**	0.43*	-0.27**	0.49*	0.74*	0.36	0.08	-0.45
III-IV	0.98**	-0.38**	-1.32**	0.66**	-0.51*	-0.22	1.13**	-0.17	0.92
Env. 3									
I-II	-0.51**	0.30**	-0.02	-0.56**	0.51*	0.29	0.34	0.29	-0.22
III-IV	0.99**	-0.35**	-0.60**	0.74**	-0.50*	0.12	0.72*	-0.20	1.08
Env. 4									
I-II	0.27**	0.43**	1.09**	0.25**	0.39	1.21**	0.14	-0.06	-0.09
III-IV	0.65**	-0.62**	-0.38*	0.57**	-0.81**	-0.23	0.12	-0.24	0.63
Env. 5									
I-II	-0.36**	0.58**	0.15	-0.43**	0.69**	0.26	0.09	0.15	0.55
III-IV	0.41**	-0.78**	-0.62**	0.13	-1.12**	0.22	0.84**	-0.44	1.15

\* indicates significance at 5%; \*\* at 1%.

Table 39. Significance of individual effects by Types within environments for ear length.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	16.70**	0.58**	6.19**	16.99**	0.64**	6.10**	0.10	0.08	-3.22**
Type II	17.36**	-0.44**	3.37**	17.29**	-0.94**	4.25**	1.03**	-0.67**	-1.42*
Type III	17.28**	0.30**	3.67**	17.13**	0.30	5.01**	1.55**	0.01	-1.67*
Type IV	17.37**	-0.59**	6.94**	17.61**	-0.46*	6.54**	-0.32	0.16	-1.86**
Env. 2									
Type I	16.29**	0.18*	5.90**	16.41**	0.73**	5.76**	-0.10	0.74**	-0.95
Type II	16.75**	-0.35**	3.36**	16.72**	-0.23	4.21**	1.03**	0.16	-1.95**
Type III	16.75**	0.39**	3.81**	16.71**	0.17	4.64**	1.01**	-0.28	-1.80**
Type IV	16.93**	-0.32**	6.33**	17.13**	-0.61**	6.44**	0.27	-0.39	-2.72**
Env. 3									
Type I	14.89**	-0.08	5.67**	15.11**	0.04	4.96**	-0.72*	0.16	-0.77
Type II	15.70**	-0.13	3.41**	15.68**	-0.06	4.24**	1.01**	0.09	-2.00**
Type III	15.36**	0.11	3.87**	15.32**	0.10	4.48**	0.72*	-0.01	-1.14
Type IV	15.49**	-0.54**	5.86**	15.80**	-0.57**	5.16**	-0.65*	-0.03	-1.83*
Env. 4									
Type I	17.12**	0.71**	6.15**	17.23**	0.80**	5.78**	-0.38	0.13	-0.26
Type II	18.31**	-0.79**	5.03**	18.31**	-0.98**	6.20**	1.44**	-0.25	-3.02**
Type III	18.20**	0.04	4.21**	17.96**	0.26	6.04**	2.09**	0.29	-1.89*
Type IV	17.82**	-0.34**	8.14**	18.01**	-0.42*	8.02**	-0.01	0.15	-1.96*
Env. 5									
Type I	13.92**	0.60**	4.23**	14.13**	0.08	4.85**	0.06	-0.69*	-2.35*
Type II	14.21**	-0.61**	3.42**	14.33**	-0.90**	4.01**	0.80	-0.39	-2.91**
Type III	14.09**	0.33*	3.14**	14.12**	0.21	3.70**	0.71	-0.16	-1.82
Type IV	14.36**	-0.20	5.65**	14.69**	-0.19	5.47**	0.00	0.01	-3.47**

\* indicates significance at 5%; \*\* at 1%.

Table 40. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for ear length.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	-0.67**	1.02**	2.82**	-0.30**	1.59**	1.85**	-0.94*	0.75*	-1.80
III-IV	-0.09	0.88**	-3.27**	-0.48**	-0.77**	-1.53**	1.86**	-0.16	0.19
Env. 2									
I-II	-0.45**	0.52**	2.54**	-0.32**	0.96**	1.54**	-1.13**	0.58*	1.00
III-IV	-0.18**	0.70**	-2.52**	-0.42**	0.78**	-1.80**	0.73*	0.11	0.92
Env. 3									
I-II	-0.81**	0.05	2.26**	-0.57**	0.10	0.72	-1.73**	0.07	1.23
III-IV	-0.13	0.65**	-1.98**	-0.48**	0.67*	-0.68	1.37**	0.02	0.63
Env. 4									
I-II	-1.19**	1.50**	1.12**	-1.08**	1.78**	-0.41	-1.82**	0.38	2.76*
III-IV	0.38**	0.58**	-3.93**	-0.05	0.68	-1.98**	2.10**	0.13	0.27
Env. 5									
I-II	-0.29*	1.21**	1.51**	-0.19*	0.98*	0.85	-0.74	-0.30	0.55
III-IV	-0.27*	0.53**	-2.51**	-0.57**	0.39	-1.77**	0.71	-0.18	1.65

\* indicates significance at 5%; \*\* at 1%.



Table 41. Significance of individual effects by Types within environments for ear diameter.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	4.50**	-0.01	0.75**	4.53**	-0.01	0.80**	0.08*	0.00	-0.49**
Type II	4.66**	0.06**	0.65**	4.67**	0.02	0.75**	0.13**	-0.06	-0.46**
Type III	4.63**	-0.09**	0.59**	4.64**	-0.12**	0.66**	0.10*	-0.04	-0.34**
Type IV	4.44**	0.08**	0.96**	4.52**	0.07*	0.90**	-0.03	-0.02	-0.74**
Env. 2									
Type I	4.37**	-0.00	0.80**	4.43**	-0.04	0.72**	-0.05	-0.05	-0.57**
Type II	4.50**	0.04**	0.79**	4.57**	0.03	0.69**	-0.08	-0.02	-0.51**
Type III	4.46**	-0.05**	0.63**	4.51**	-0.13**	0.61**	0.01	-0.11**	-0.48**
Type IV	4.31**	0.08**	0.94**	4.40**	0.06*	0.84**	-0.06	-0.02	-0.80**
Env. 3									
Type I	4.16**	-0.00	0.75**	4.21**	-0.04	0.59**	-0.16**	-0.05	-0.15
Type II	4.37**	0.04**	0.78**	4.44**	0.04	0.63**	-0.13**	-0.00	-0.37**
Type III	4.32**	-0.06**	0.57**	4.35**	-0.07*	0.51**	-0.04	-0.02	-0.28*
Type IV	4.16**	0.10**	0.90**	4.21**	0.09**	0.90**	0.04	-0.01	-0.68**
Env. 4									
Type I	4.38**	0.03*	0.78**	4.41**	-0.04	0.77**	0.01	-0.10**	-0.34**
Type II	4.49**	0.06**	0.69**	4.51**	0.05	0.72**	0.05	-0.01	-0.31**
Type III	4.47**	-0.09**	0.66**	4.49**	-0.11**	0.71**	0.08	-0.03	-0.36**
Type IV	4.29**	0.09**	0.97**	4.35**	0.09**	0.95**	0.02	0.01	-0.65**
Env. 5									
Type I	3.91**	0.03	0.75**	3.96**	-0.00	0.65**	-0.09	-0.04	-0.38**
Type II	4.10**	0.01	0.71**	4.14**	0.02	0.69**	0.00	0.01	-0.43**
Type III	3.96**	-0.04*	0.67**	4.01**	-0.12**	0.67**	0.04	-0.11*	-0.59**
Type IV	3.86**	0.12**	0.80**	3.92**	0.14**	0.69**	-0.09	0.03	-0.45**

\* indicates significance at 5%; \*\* at 1%.

Table 42. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for ear diameter.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	-0.15**	-0.07**	0.10**	-0.14**	-0.03	0.06	-0.04	0.06	-0.03
III-IV	0.18**	-0.17**	-0.37**	0.12**	-0.19**	-0.24**	0.12*	-0.02	0.40**
Env. 2									
I-II	-0.13**	-0.04*	0.01	-0.13**	-0.07	0.03	0.02	-0.04	-0.06
III-IV	0.15**	-0.13**	-0.31**	0.11**	-0.19**	-0.23**	0.07	-0.09	0.32*
Env. 3									
I-II	-0.21**	-0.05*	-0.03	-0.23**	-0.08	-0.04	-0.03	-0.05	0.22
III-IV	0.16**	-0.16**	-0.33**	0.14**	-0.17**	-0.39**	-0.08	-0.01	0.40*
Env. 4									
I-II	-0.10**	-0.02	0.09*	-0.09**	-0.09*	0.05	-0.04	-0.09	-0.03
III-IV	0.18**	-0.18**	-0.31**	0.13**	-0.21**	-0.23**	0.06	-0.04	0.28
Env. 5									
I-II	-0.20**	0.01	0.05	-0.18**	-0.02	-0.04	-0.09	-0.04	0.05
III-IV	0.10**	-0.16**	-0.14**	0.08**	-0.26**	-0.02	0.13	-0.14*	-0.14

\* indicates significance at 5%; \*\* at 1%.

Table 43. Significance of individual effects by Types within environments for yield.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	124.27**	2.05	123.76**	125.17**	1.31	130.14**	8.48	-0.99	-27.29*
Type II	136.80**	-5.53**	110.14**	136.42**	-15.55**	134.71**	30.00**	-13.37**	-59.50**
Type III	135.79**	4.05**	97.78**	135.31**	4.04	112.45**	17.75**	-0.01	-32.70**
Type IV	126.39**	-6.99**	142.69**	128.17**	-6.62*	150.17**	10.46*	0.48	-40.56**
Env. 2									
Type I	105.64**	2.11	122.15**	106.27**	2.09	123.04**	1.53	-0.03	-9.79
Type II	114.42**	-1.97	110.42**	116.61**	2.53	124.95**	19.42**	6.00	-63.73**
Type III	113.51**	5.35**	94.87**	114.06**	5.73	103.30**	10.76*	0.52	-28.42*
Type IV	101.17**	-0.70	133.99**	101.01**	-1.00	149.52**	19.02**	-0.39	-38.59**
Env. 3									
Type I	81.69**	-2.32	86.71**	80.48**	-1.77	85.77**	-2.00	0.73	16.78
Type II	95.45**	-1.28	83.79**	94.76**	-0.41	101.70**	21.58**	1.17	-38.53**
Type III	88.91**	2.49	74.05**	90.25**	1.38	83.15**	12.14*	-1.47	-39.55**
Type IV	81.71**	-4.18**	106.85**	81.43**	-2.75	115.22**	10.10*	1.91	-18.50
Env. 4									
Type I	127.53**	3.69*	112.41**	127.19**	1.57	116.43**	4.71	-2.83	-6.48
Type II	142.54**	-3.41*	120.43**	142.69**	-9.83**	138.09**	21.85**	-8.55*	-47.83**
Type III	139.19**	1.64	100.82**	138.21**	2.06	112.68**	13.93**	0.56	-19.32
Type IV	127.32**	-2.36	149.85**	129.51**	-1.35	161.90**	16.37**	1.35	-57.38**
Env. 5									
Type I	66.39**	2.58	73.36**	67.31**	-1.94	74.47**	2.02	-6.02	-13.82
Type II	74.16**	-1.63	75.17**	74.38**	-1.63	84.59**	11.76*	-0.00	-27.18*
Type III	68.63**	3.02*	62.29**	67.86**	0.90	74.53**	14.54**	-2.82	-22.82
Type IV	66.71**	-0.11	80.77**	69.03**	-0.20	88.37**	10.98*	-0.13	-47.33**

\* indicates significance at 5%; \*\* at 1%.

Table 44. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for yield.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	-12.54**	7.58**	13.62**	-11.25**	16.86**	-4.57	-21.51**	12.37*	32.21
III-IV	9.40**	11.03**	-44.91**	7.15**	10.67*	-37.72**	7.29	-0.49	7.85
Env. 2									
I-II	-8.78**	4.09*	11.73**	-10.33**	-0.44	-1.92	-17.89**	-6.03	53.94**
III-IV	12.34**	6.05**	-39.12**	13.04**	6.73	-46.22**	-8.26	0.91	10.17
Env. 3									
I-II	-13.76**	-1.04	2.92	-14.27**	-1.37	-15.93*	-23.58**	-0.44	55.31**
III-IV	7.20**	6.67**	-32.81**	8.82**	4.14	-32.07**	2.04	-3.38	-21.04
Env. 4									
I-II	-15.01**	7.10**	-8.02*	-15.50**	11.39*	-21.66**	-17.14*	5.72	41.35*
III-IV	11.87**	4.01	-49.03**	8.69**	3.41	-49.22**	-2.44	-0.79	38.06*
Env. 5									
I-II	-7.77**	4.21	-1.81	-7.06**	-0.31	-10.12	-9.74	-6.02	13.35
III-IV	1.92**	3.12	-18.48**	-1.18	1.10	-12.84	3.56	-2.69	24.51

\* indicates significance at 5%; \*\* at 1%.

Table 45. Significance of individual effects by Types within environments for 300-kernel weight.

Environment Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
Type I	76.01**	-2.10**	15.87**	76.22**	-3.77**	17.57**	2.25	-2.23	-7.01
Type II	82.14**	3.71**	13.65**	81.55**	5.30**	20.74**	8.33**	2.13	-11.60**
Type III	76.09**	-3.57**	3.32**	75.16**	-6.98**	6.93**	3.80*	-4.55**	1.67
Type IV	78.95**	2.88**	5.52**	77.47**	6.65**	13.08**	8.29**	1.02	-2.23
Env. 2									
Type I	75.03**	-1.44*	7.66**	75.45**	-2.48	9.29**	2.30	-1.38	-9.21
Type II	78.07**	4.94**	7.64**	76.89**	7.30**	10.43**	2.61	3.14*	6.67
Type III	71.48**	-4.81**	0.95	70.69**	-8.97**	1.70	0.38	-5.54**	7.41
Type IV	77.03**	3.53**	-2.51*	74.76**	4.61**	8.08**	11.46**	1.44	-0.74
Env. 3									
Type I	71.33**	0.50	8.22**	72.01**	0.38	7.19**	-0.80	-0.16	-5.29
Type II	75.00**	3.54**	3.14**	74.07**	5.61**	6.20**	3.13	2.75	2.98
Type III	67.84**	-5.49**	-1.57	67.41**	-6.17**	0.87	2.71	-0.90	-1.30
Type IV	75.39**	4.01**	0.76	74.37**	3.45**	11.20**	12.14**	-0.74	-15.15**
Env. 4									
Type I	71.05**	-1.79**	15.69**	71.75**	-3.29**	16.85**	1.92	-2.00	-11.36*
Type II	77.13**	4.87**	14.67**	75.86**	5.31**	22.46**	8.72**	0.59	-5.37
Type III	70.64**	-3.38**	8.52**	70.11**	-7.27**	10.68**	2.29	-5.18**	0.65
Type IV	71.81**	-1.19*	10.99**	70.99**	0.06	16.18**	5.82**	1.66	-3.76
Env. 5									
Type I	58.77**	-0.90	15.63**	58.79**	-0.52	14.87**	-0.93	0.51	1.78
Type II	66.51**	4.45**	17.24**	65.59**	4.66**	23.59**	7.18**	0.28	-5.60
Type III	59.50**	-2.04**	13.78**	58.81**	-4.40**	14.74**	0.71	-3.14*	5.60
Type IV	61.07**	-0.48	4.16**	59.21**	4.56**	13.51**	10.22**	6.72**	-2.37

\* indicates significance at 5%; \*\* at 1%.

Table 46. Significance of differences between individual effects of Types I and II, and Types III and IV within environments for 300-kernel weight.

Environment Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Env. 1									
I-II	-6.13**	-5.80**	2.22	-5.33**	-9.07**	-3.17	-6.08*	-4.36*	4.59
III-IV	-2.85**	-6.45**	-2.20	-2.31**	-10.63**	-6.15*	-4.49	-5.57**	3.89
Env. 2									
I-II	-3.03**	-6.38**	0.02	-1.43*	-9.77*	-1.14	-0.31	-4.52*	-15.88*
III-IV	-5.55**	-8.43**	3.46*	-4.07**	-13.57**	-6.37*	-11.08**	-6.97**	8.15
Env. 3									
I-II	-3.67**	-3.05**	5.09**	-2.07**	-5.23**	0.99	-3.93	-2.91	-8.27
III-IV	-7.55**	-9.50**	-2.34	-6.96**	-9.62**	-10.33**	-9.43**	-0.16	13.85*
Env. 4									
I-II	-6.08**	-6.66**	1.02	-4.11**	-8.61**	-5.61*	-6.79*	-2.59	-5.98
III-IV	-1.17*	-2.19**	-2.47	-0.88	-7.33**	-5.50*	-3.52	-6.84**	4.41
Env. 5									
I-II	-7.74**	-5.35**	-1.61	-6.79**	-5.18**	-8.73**	-8.11**	0.22	7.38
III-IV	-1.57**	-1.56	9.62**	-0.39	-8.96**	1.24	-9.51**	-9.86**	7.97

\* indicates significance at 5%; \*\* at 1%.

Table 47. Standard error of an effect pooled over crosses within a Type for a given environment.

Character Environment	df	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Date silk										
Env. 1	11634	0.09	0.14	0.28	0.12	0.31	0.48	0.47	0.37	1.15
Env. 2										
Env. 3										
Env. 4	11907	0.08	0.13	0.25	0.11	0.28	0.43	0.43	0.33	1.04
Env. 5										
Plant height										
Env. 1	11613	0.40	0.63	1.24	0.52	1.38	2.15	2.10	1.64	5.14
Env. 2	11886	0.37	0.57	1.13	0.48	1.26	1.96	1.92	1.50	4.69
Env. 3	11886	0.38	0.60	1.18	0.50	1.32	2.05	2.00	1.56	4.90
Env. 4	11928	0.38	0.59	1.17	0.49	1.30	2.02	1.98	1.54	4.83
Env. 5	11802	0.62	0.97	1.92	0.81	2.14	3.32	3.25	2.54	7.96
Ear height										
Env. 1	11613	0.32	0.49	0.98	0.41	1.09	1.69	1.66	1.29	4.05
Env. 2	11886	0.32	0.50	0.99	0.42	1.10	1.72	1.68	1.31	4.11
Env. 3	11886	0.28	0.43	0.85	0.36	0.95	1.48	1.45	1.13	3.54
Env. 4	11928	0.32	0.50	0.99	0.42	1.10	1.71	1.68	1.31	4.10
Env. 5	11739	0.45	0.70	1.38	0.58	1.53	2.39	2.33	1.82	5.71
Kernel row no.										
Env. 1	11130	0.04	0.06	0.12	0.05	0.13	0.21	0.20	0.16	0.50
Env. 2	11025	0.04	0.07	0.13	0.05	0.15	0.23	0.22	0.17	0.54
Env. 3	10122	0.04	0.07	0.13	0.05	0.15	0.23	0.22	0.17	0.55
Env. 4	11865	0.04	0.07	0.13	0.06	0.15	0.23	0.23	0.17	0.55
Env. 5	11403	0.04	0.07	0.13	0.06	0.15	0.23	0.23	0.18	0.55

Table 47. (Continued)

Character		Model 1			Model 2					
Environment	df	m	a	d	m	a	d	aa	ad	dd
<hr/>										
Ear length										
Env. 1	11130	0.05	0.08	0.17	0.07	0.19	0.29	0.29	0.22	0.70
Env. 2	11025	0.05	0.08	0.15	0.06	0.17	0.26	0.26	0.20	0.63
Env. 3	10122	0.06	0.09	0.19	0.08	0.21	0.32	0.31	0.25	0.77
Env. 4	11865	0.06	0.09	0.19	0.08	0.21	0.33	0.32	0.25	0.78
Env. 5	11403	0.08	0.13	0.26	0.11	0.29	0.46	0.45	0.35	1.09
Ear diameter										
Env. 1	11130	0.01	0.01	0.02	0.01	0.03	0.04	0.04	0.03	0.10
Env. 2	11025	0.01	0.01	0.02	0.01	0.03	0.04	0.04	0.03	0.10
Env. 3	10122	0.01	0.01	0.03	0.01	0.03	0.05	0.05	0.04	0.12
Env. 4	11865	0.01	0.01	0.03	0.01	0.03	0.05	0.05	0.04	0.12
Env. 5	11403	0.01	0.02	0.03	0.01	0.04	0.06	0.05	0.04	0.13
Yield										
Env. 1	11067	0.97	1.52	3.02	1.28	3.36	5.23	5.12	3.99	12.51
Env. 2	11004	0.89	1.39	2.75	1.16	3.05	4.75	4.65	3.63	11.36
Env. 3	10101	0.98	1.53	3.03	1.28	3.37	5.23	5.13	4.00	12.53
Env. 4	11865	0.93	1.45	2.88	1.21	3.20	4.97	4.87	3.80	11.91
Env. 5	11340	0.98	1.54	3.05	1.29	3.39	5.27	5.17	4.03	12.63
300-kernel wt.										
Env. 1	11025	0.33	0.52	1.03	0.44	1.15	1.79	1.75	1.37	4.28
Env. 2	11004	0.37	0.57	1.14	0.48	1.27	1.97	1.93	1.50	4.71
Env. 3	10101	0.35	0.55	1.08	0.46	1.21	1.87	1.84	1.43	4.49
Env. 4	11697	0.36	0.56	1.11	0.47	1.23	1.92	1.88	1.47	4.59
Env. 5	11340	0.37	0.58	1.15	0.49	1.28	1.99	1.95	1.52	4.76



for Types II and III and  $\hat{d}\hat{d}$  for Types II, III, and IV. Significant differences for the two comparisons were in the majority for  $\hat{m}$ ,  $\hat{a}$ ,  $\hat{d}$ , and  $\hat{a}\hat{a}$  (Tables 39 and 40).

All Types in all, or nearly all, environments showed significant  $\hat{m}$ ,  $\hat{d}$ , and  $\hat{d}\hat{d}$  for ear diameter. Types II, III, and IV were significant for  $\hat{a}$ . The first comparison of Types revealed differences in  $\hat{m}$  and  $\hat{d}$  for more than half the environments. Type III versus Type IV resulted in significance for  $\hat{m}$ ,  $\hat{a}$ ,  $\hat{d}$ , and  $\hat{d}\hat{d}$  in at least three environments (Tables 41 and 42).

As with most of the other characters, yield also was significant for  $\hat{m}$  and  $\hat{d}$  in all Type-environment combinations. Significant  $\hat{a}$  occurred sporadically, but Type III was the only Type to have it present in at least three environments. All but Type I showed significant  $\hat{a}\hat{a}$  in each environment and, likewise, in the majority of environments for  $\hat{d}\hat{d}$ . Significant differences for both comparisons were shown for  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$ . The first comparison also had real differences for  $\hat{a}\hat{a}$  and  $\hat{d}\hat{d}$  (Tables 43 and 44).

The significant individual effects for 300-kernel weight in most environments for all Types were  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$ . Types II and IV had significant  $\hat{a}\hat{a}$  effects and Type III showed  $\hat{a}\hat{d}$ . The differences for the two comparisons, which were of larger importance, were for  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{a}\hat{a}$ .  $\hat{a}\hat{d}$  was of importance only in the second comparison (Tables 45 and 46).

Effects from the combined analyses of variance over environments, by Types for each character, are listed in Tables 67 through 74 in the Appendix. Standard errors for these effects are in Table 75 in the Appendix.

Tables 48 through 51 present the frequency of significant effects by Types for Model 1 and Model 2 combined over the five environments. The previous comment on confounding of  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$  in Model 2, where epistasis

is present, should be reemphasized. All characters, in all Types, were significant for  $\hat{m}$  in 21 of 21 crosses. Except for kernel row number and 300-kernel weight, all crosses in all Types were significant for  $\hat{d}$ . The occurrence of significant  $\hat{a}$  effects was high (over two-thirds of the crosses), but not nearly as high as for  $\hat{d}$ .

Type IV had fewer instances of significant  $\hat{a}$  than Type III for date silk. Type I had more occurrences of each one of the epistatic effects than did Type II, the former being about one-third of the crosses and the latter less than one-seventh. Type IV showed less  $\hat{aa}$ ,  $\hat{ad}$ , and  $\hat{dd}$  than Type III.

Examination of plant and ear height effects revealed about equal occurrences of significant  $\hat{a}$  for Types I, III, and IV, with Type II showing relatively fewer occurrences. Types I and II had similar frequencies of  $\hat{aa}$  and  $\hat{dd}$ , with more instances of  $\hat{ad}$  in Type I for plant height. Considerably more epistasis was present in Type IV than Type III, especially for  $\hat{dd}$ , which was approximately five times more frequent in Type IV than Type III.

Kernel row number  $\hat{a}$  effects were shown more by Types I and IV than Types II and III. Types I and II had 19 of 21 crosses significant for  $\hat{d}$  versus 21 of 21 for Types III and IV. Somewhat more epistasis was present in Type II than Type I and considerably more for Type IV than Type III.

Ear length and diameter had approximately the same frequency of  $\hat{a}$  significance for all Types; except Type II for ear length, in which  $\hat{a}$  significance was slightly more frequent. More epistasis, particularly  $\hat{aa}$ , was shown by Type II than I for ear length. Type IV ear length favored more  $\hat{dd}$  than Type III and the remaining epistatic terms were also more important for Type IV. For ear diameter, instances of  $\hat{aa}$  and  $\hat{ad}$  were equal and  $\hat{dd}$

was more prevalent in Type II than Type I. Again, Type IV had considerably more occurrences of  $\hat{a}\hat{a}$  and  $\hat{d}\hat{d}$  than did Type III.  $\hat{a}\hat{d}$  effects were equally frequent and occurred in about half of the crosses in Types III and IV.

Two-thirds of the crosses for yield demonstrated a significant  $\hat{a}$  effect in all Types. Type II exhibited much more epistasis than Type I when all three epistatic terms were considered.  $\hat{a}\hat{a}$  and  $\hat{d}\hat{d}$  were very much more in evidence for Type II, while there was only a slightly more frequent occurrence of  $\hat{a}\hat{d}$  in Type I. Surprisingly, levels of all epistatic effects in Types III and IV were very close to one-third.

300-kernel weight had similar numbers of crosses significant for  $\hat{a}$  in Types II, III, and IV. Fewer crosses had a significant estimate of  $\hat{a}$  in Type I than the other Types.  $\hat{d}$  was significant for nearly all crosses in Types I and II, and occurred 16 and 11 times in Types III and IV, respectively. The frequency of epistasis was greater in Type II than Type I for  $\hat{a}\hat{a}$  and  $\hat{a}\hat{d}$ , and the reverse for  $\hat{d}\hat{d}$ . Type III had more occurrences of  $\hat{a}\hat{d}$  and  $\hat{d}\hat{d}$  than Type IV, but Type IV had significant  $\hat{a}\hat{a}$  in 15 crosses versus three for Type III.

Two sets of tables have been presented dealing with the frequency of significant effects for the 21 crosses in a Type. The first were for crosses in each environment and the second were for crosses combined over environments. Comments made on those counts were based primarily on the 5% level of significance. The application of a 1% level of significance had little effect on the number of crosses significant for  $\hat{d}$ . It reduced the number for  $\hat{a}$  slightly and, in some cases, drastically reduced the occurrence of significant epistasis. Overall, however, significant epistasis was reduced only a bit more than for the  $\hat{a}$  effect. Counts of signif-

Table 48. Number of crosses out of 21 in each Type combined over environments which show significant individual effects at 5% for date silk, plant height, ear height, and kernel row number.

Character Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Date silk									
Type I	21	17	21	21	17	20	9	5	7
Type II	21	17	21	21	12	19	2	1	3
Type III	21	19	21	21	13	21	6	3	5
Type IV	21	12	21	21	11	21	3	1	1
Plant height									
Type I	21	17	21	21	15	21	9	7	8
Type II	21	13	21	21	8	21	10	3	10
Type III	21	16	21	21	12	21	3	5	2
Type IV	21	18	21	21	16	21	6	9	12
Ear height									
Type I	21	19	21	21	19	21	9	5	8
Type II	21	12	21	21	10	21	8	5	7
Type III	21	17	21	21	10	21	4	6	2
Type IV	21	19	21	21	14	21	6	6	10
Kernel row number									
Type I	21	20	19	21	15	16	1	2	3
Type II	21	10	19	21	8	14	2	8	4
Type III	21	11	21	21	7	18	1	4	4
Type IV	21	18	21	21	17	15	8	10	10

Table 49. Number of crosses out of 21 in each Type combined over environments which show significant individual effects at 1% for date silk, plant height, ear height, and kernel row number.

Character Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Date silk									
Type I	21	17	21	21	14	19	7	4	4
Type II	21	15	21	21	9	19	2	0	1
Type III	21	18	21	21	13	18	2	3	2
Type IV	21	11	21	21	10	21	1	0	1
Plant height									
Type I	21	17	21	21	13	21	5	7	4
Type II	21	11	21	21	8	21	5	2	6
Type III	21	15	21	21	8	21	2	1	1
Type IV	21	18	21	21	13	21	3	9	6
Ear height									
Type I	21	18	21	21	17	21	6	2	6
Type II	21	8	21	21	8	21	4	5	5
Type III	21	16	21	21	8	21	2	3	1
Type IV	21	17	21	21	14	21	4	1	5
Kernel row number									
Type I	21	19	19	21	12	13	1	1	1
Type II	21	7	17	21	6	4	1	5	0
Type III	21	11	20	21	3	15	0	2	2
Type IV	21	18	21	21	12	13	7	8	7

Table 50. Number of crosses out of 21 in each Type combined over environments which show significant individual effects at 5% for ear length, ear diameter, yield, and 300-kernel weight.

Character Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Ear length									
Type I	21	16	21	21	15	21	3	5	6
Type II	21	19	21	21	15	21	12	6	8
Type III	21	17	21	21	10	21	8	2	6
Type IV	21	16	21	21	13	21	9	5	10
Ear diameter									
Type I	21	16	21	21	12	21	6	7	7
Type II	21	15	21	21	9	21	4	9	11
Type III	21	15	21	21	10	21	2	11	8
Type IV	21	17	21	21	12	21	10	11	14
Yield									
Type I	21	14	21	21	5	21	2	6	2
Type II	21	15	21	21	7	21	13	4	10
Type III	21	14	21	21	8	21	7	7	6
Type IV	21	15	21	21	8	21	6	6	6
300-kernel weight									
Type I	21	14	20	21	11	15	4	1	4
Type II	21	17	21	21	14	20	9	6	2
Type III	21	16	16	21	13	13	3	9	5
Type IV	21	17	11	21	14	15	15	6	1

Table 51. Number of crosses out of 21 in each Type combined over environments which show significant individual effects at 1% for ear length, ear diameter, yield, and 300 kernel weight.

Character Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Ear length									
Type I	21	14	21	21	14	21	1	2	2
Type II	21	19	20	21	10	21	9	6	3
Type III	21	17	20	21	7	21	5	0	4
Type IV	21	15	21	21	12	21	5	4	7
Ear diameter									
Type I	21	16	21	21	11	21	1	3	4
Type II	21	13	21	21	6	21	2	6	6
Type III	21	13	21	21	10	21	0	6	5
Type IV	21	17	21	21	6	21	5	6	13
Yield									
Type I	21	10	21	21	3	21	1	2	1
Type II	21	13	21	21	6	21	7	4	7
Type III	21	11	21	21	3	21	4	5	3
Type IV	21	12	21	21	3	21	4	4	5
300-kernel weight									
Type I	21	13	17	21	7	13	2	0	2
Type II	21	16	20	21	12	20	4	1	1
Type III	21	15	11	21	12	9	2	6	1
Type IV	21	16	10	21	11	13	11	5	1

ificance for  $\hat{a}$  and  $\hat{ad}$  were not biased by any cancelling of effects due to  $P_1$  and  $P_2$  assignment, since no pooling over crosses occurred.

Combined effects, pooled over the crosses within a Type, are given in Table 52. The two comparisons of differences, Type I versus Type II and Type III versus Type IV, follow in Table 53 and the standard errors of the effects are in Table 54. Every Type for every character had a significant  $\hat{m}$  effect. Likewise,  $\hat{a}$  was significant in all cases except ear diameter for Type I and  $\hat{d}$  in all cases except 300-kernel weight for Type IV.

All Types, for date silk, had a significant  $\hat{aa}$  effect. No Types were significant for  $\hat{ad}$  and all but Type I were for  $\hat{dd}$ . Plant and ear height were found to have a significant  $\hat{aa}$  effect for Types I and III,  $\hat{dd}$  for Types I, II, and IV, and  $\hat{ad}$  for Types I and II. Type IV crosses for plant height also demonstrated significant  $\hat{ad}$  effects. Kernel row number epistatic effects which were of significance were  $\hat{aa}$  and  $\hat{ad}$  for Types II and IV and  $\hat{dd}$  for all Types.  $\hat{aa}$  was significant in Types II and III for ear length. The estimate of  $\hat{dd}$  for ear length was significant in all Types, as was the estimate of  $\hat{dd}$  for ear diameter. Further epistasis for ear diameter was shown in Type I for  $\hat{aa}$  and  $\hat{ad}$ , and in Type III for  $\hat{ad}$ . Yield showed no significant  $\hat{ad}$ , but did have significant  $\hat{aa}$  and  $\hat{dd}$  effects for Types II, III, and IV. The last three Types, for 300-kernel weight, were significant for  $\hat{aa}$  and  $\hat{ad}$ . Only Types I and IV were significant for  $\hat{dd}$ .

Dominance effects were positive for all characters but date silk. The  $\hat{dd}$  effects were negative for all except date silk. Additive x additive effects were all positive for plant height, yield, and 300-kernel weight and negative for date silk. Otherwise, the signs of effects differed from Type to Type for each character.



Dominance effects were of the same magnitude as  $\hat{m}$  for yield and added substantially to plant height, ear height, and ear length. Additive  $\times$  additive and dominance  $\times$  dominance effects were of major importance for yield when relative magnitudes were considered; however, due to differing signs, the net effect was small.

Comparison of Type I versus Type II for date silk showed that all effects except  $\hat{d}$  and  $\hat{aa}$  were different. The second comparison, Type III versus Type IV, was significant only for  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$ .

Plant height, for the first comparison, had differences only in  $\hat{m}$  and  $\hat{a}$ . Type III versus Type IV was significant for all but  $\hat{aa}$  and  $\hat{ad}$ . Ear height was significant for  $\hat{m}$  and  $\hat{d}$  in both comparisons. The first ear height comparison also had significant differences for  $\hat{a}$  and  $\hat{aa}$ , while the second was significant for  $\hat{dd}$ .

The kernel row number and ear diameter comparisons were significant for  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$ . The first comparison had no significant epistasis, whereas, the second was significant for all three epistatic effects. Ear length showed no difference for  $\hat{m}$  in the second comparison.  $\hat{a}$ ,  $\hat{d}$ , and  $\hat{aa}$  were significantly different in both of the comparisons.

Differences for  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$  were found for the two yield comparisons. Of the epistatic effects, only  $\hat{aa}$  and  $\hat{dd}$  were significant for the first comparison and none were significant for the second. The first 300-kernel weight comparison was significant for all but  $\hat{d}$  and  $\hat{dd}$  and the second for all but  $\hat{d}$ .

Examination of the estimates of  $\hat{m}$  characterized Type II, as opposed to Type I, as having earlier maturity, shorter plant and ear height, larger ears with more kernel rows, more yield, and heavier kernels. Similarly,

Table 52. Significance of individual effects by Types combined over environments.

Character Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Date silk									
Type I	33.27**	0.25**	-7.10**	33.46**	0.53*	-7.79**	-0.71*	0.38	-0.50
Type II	30.75**	-0.38**	-6.73**	30.72**	-0.67**	-7.28**	-0.71*	-0.39	1.91*
Type III	30.44**	-0.44**	-5.80**	30.25**	-0.69**	-6.74**	-1.29**	-0.34	4.72**
Type IV	33.57**	1.26**	-7.54**	33.58**	1.27**	-8.61**	-1.31**	0.00	2.67**
Plant height									
Type I	200.41**	2.02**	58.65**	201.53**	0.37	60.01**	2.46*	-2.20**	-16.77**
Type II	184.92**	-5.70**	58.47**	186.94**	-7.60**	58.10**	0.96	-2.53**	-22.90**
Type III	178.06**	0.69*	51.16**	177.92**	1.04	53.64**	2.95**	0.46	-4.72
Type IV	193.47**	-2.76**	65.68**	195.77**	-1.08	65.12**	0.91	2.24**	-25.76**
Ear height									
Type I	101.39**	1.03**	31.92**	101.78**	-0.15	35.19**	4.31**	-1.59*	-13.23**
Type II	76.44**	-4.68**	33.52**	77.74**	-6.06**	32.18**	-0.74	-1.85**	-11.87**
Type III	73.96**	2.14**	28.78**	73.49**	2.41**	30.33**	1.59*	0.36	1.48
Type IV	84.50**	1.72**	36.92**	86.11**	2.47**	36.23**	0.27	1.00	-17.25**
Kernel row no.									
Type I	15.16**	0.15**	1.71**	15.26**	0.07	1.58**	-0.09	-0.11	-0.87**
Type II	15.37**	-0.25**	1.33**	16.53**	-0.45**	0.98*	-0.32**	-0.27**	-0.98**
Type III	15.73**	0.13**	1.71**	15.83**	0.13*	1.66**	0.01	0.01	-1.02**
Type IV	14.93**	0.65**	2.41**	15.25**	0.83**	1.73**	-0.61**	0.24**	-1.98**

\* indicates significance at 5%; \*\* at 1%.

Table 52. (Continued)

Character Type	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Ear length									
Type I	15.78**	0.40**	5.77**	15.97**	0.46**	5.49**	-0.21	0.08	-1.51**
Type II	16.47**	-0.46**	3.72**	16.47**	-0.62**	4.58**	1.06**	-0.21	-2.26**
Type III	16.34**	0.23**	3.74**	16.25**	0.21*	4.77**	1.21**	-0.03	-1.67**
Type IV	16.39**	-0.44**	6.58**	16.65**	-0.45**	6.33**	-0.14	-0.02	-2.37**
Ear diameter									
Type I	4.26**	0.01	0.77**	4.31**	-0.03	0.71**	-0.04*	-0.05**	-0.39**
Type II	4.42**	0.04**	0.72**	4.47**	0.03*	0.69**	-0.01	-0.02	-0.41**
Type III	4.37**	-0.07**	0.62**	4.40**	-0.11**	0.63**	0.04	-0.06**	-0.41**
Type IV	4.21**	0.09**	0.91**	4.28**	0.09**	0.85**	-0.02	-0.00	-0.66**
Yield									
Type I	101.11**	1.62*	103.68**	101.29**	0.25	105.97**	2.95	-1.83	-8.12
Type II	112.68**	-2.77**	99.99**	112.97**	-4.98**	116.81**	20.92**	-2.95	-47.35**
Type III	109.21**	3.31**	85.96**	109.14**	2.83	97.22**	13.82**	-0.64	-28.56**
Type IV	100.66**	-2.87**	122.83**	101.83**	-2.39	133.04**	13.39**	0.64	-40.47**
300-kernel wt.									
Type I	70.44**	-1.15**	12.61**	70.85**	-1.94**	13.15**	0.95	-1.05	-6.22**
Type II	75.77**	4.30**	11.27**	74.79**	5.63**	16.69**	5.99**	1.78**	-2.59
Type III	69.11**	-3.86**	5.00**	68.44**	-6.76**	6.98*	1.98*	-3.86**	2.80
Type IV	72.85**	1.75**	3.78	71.36**	3.27**	12.41**	9.59**	2.02**	-4.85*

Table 53. Significance of differences between individual effects of Types I and II, and Types III and IV combined over environments.

Character Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Date silk									
I-II	2.51**	0.63**	-0.37	2.75**	1.21**	-0.51	-0.00	0.77*	-2.41*
III-IV	-3.13**	-1.70**	1.74**	-3.33**	-1.96**	1.87**	0.02	-0.34	2.05
Plant height									
I-II	15.49**	7.72**	0.18	14.59**	7.97**	1.91	1.50	0.33	6.13
III-IV	-15.40**	3.46**	-14.51**	-17.85**	2.12*	-11.48**	2.04	-1.78	21.03**
Ear height									
I-II	24.94**	5.71**	-1.60*	24.04**	5.91**	3.01**	5.05**	0.26	-1.36
III-IV	-10.53**	0.42	-8.15**	-12.61**	-0.06	-5.90**	1.32	-0.63	18.73**
Kernel row no.									
I-II	-0.21**	0.40**	0.38**	-0.27**	0.52**	0.60**	0.23	0.15	0.11
III-IV	0.80**	-0.52**	-0.69**	0.58**	-0.70**	-0.07	0.62**	-0.23*	0.96**
Ear length									
I-II	-0.68**	0.86**	2.05**	-0.49**	1.08**	0.91**	-1.27**	0.29	0.75
III-IV	-0.06	0.67**	-2.84**	-0.40**	0.66**	-1.55**	1.35**	-0.01	0.70
Ear diameter									
I-II	-0.16**	-0.03**	0.05*	-0.15**	-0.06**	0.01	-0.03	-0.03	0.03
III-IV	0.15**	-0.16**	-0.29**	0.12**	-0.20**	-0.22**	0.06*	-0.06*	0.25**

\* indicates significance at 5%; \*\* at 1%.

Table 53. (Continued)

Character Types	Model 1			Model 2					
	m	a	d	m	a	d	aa	ad	dd
Yield									
I-II	-11.57**	4.39**	3.69*	-11.68**	5.23*	-10.84**	-17.97**	1.12	39.23**
III-IV	8.55**	6.18**	-36.87**	7.31**	5.21*	-35.81**	0.44	-1.29	11.91
300-kernel wt.									
I-II	-5.33**	-5.45**	1.35	-3.95**	-7.57**	-3.53**	-5.05**	-2.83**	-3.63
III-IV	-3.74**	-5.61**	1.21	-2.92**	-10.02**	-5.42**	-7.61**	-5.88**	7.65**

Table 54. Standard error of an effect combined over environments and pooled over crosses within a Type

Character	df	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Date silk	23541	0.06	0.09	0.19	0.08	0.21	0.32	0.32	0.25	0.77
Plant height	59115	0.20	0.31	0.61	0.26	0.68	1.05	1.03	0.81	2.52
Ear height	59052	0.15	0.24	0.47	0.20	0.52	0.81	0.80	0.62	1.95
Kernel row no.	55545	0.02	0.03	0.06	0.02	0.06	0.10	0.10	0.08	0.24
Ear length	55545	0.03	0.04	0.09	0.04	0.10	0.15	0.15	0.12	0.36
Ear diameter	55545	0.004	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.05
Yield	55377	0.43	0.66	1.32	0.56	1.46	2.28	2.23	1.74	5.45
300-kernel wt.	55167	0.16	0.25	0.49	0.21	0.55	0.85	0.84	0.65	2.04

the comparison of Types III and IV showed that Type III had earlier maturity, shorter plants, lower ears, more kernel rows, a longer ear, higher yield, and lighter kernels. These results are in excellent agreement with data already presented for observed values on both  $F_1$ 's and the average of the parents.

#### Correlation Analyses

Simple product-moment correlations were computed for each Type in each character. Correlations were among observed and predicted values by Model 1 and Model 2 over the five environments. The number of pairs of values entering each correlation coefficient was 189, obtained as described in the statistical procedures section. With an  $n = 189$ , the observed value must exceed 0.19 for significance at .01 probability level. All of the coefficients exceeded 0.19 by a considerable margin.

The correlations of observed values and predicted values in each environment and averaged over environments are shown in Table 55. Considering Model 1 only, the greatest spread between two environments was 0.182 occurring in Type III for kernel row number. Except for kernel row number, most of the differences between environments were no larger than 0.05. Fitting the epistatic terms increased the correlation about 0.02 for plant height and ear height, 0.03 for date silk and yield, 0.05 for kernel row number and ear length, and 0.06 for ear diameter and 300-kernel weight. Plant and ear height had the highest correlations and the lowest were for kernel row number and 300-kernel weight. In some cases there was strikingly little parallel between high and low correlations of the two models, e.g., date silk in environment 1.

Table 55. Correlation of observed values with predicted values for Model 1 (M1) and Model 2 (M2) in each environment by Type.

Character Type	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5		Average	
	M1	M2	M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Date silk												
Type I	.945	.980					.947	.982			.946	.981
Type II	.958	.979					.976	.987			.967	.983
Type III	.952	.979					.969	.985			.961	.982
Type IV	.961	.980					.963	.983			.962	.981
Plant height												
Type I	.971	.988	.978	.990	.968	.988	.975	.990	.940	.969	.966	.985
Type II	.965	.990	.966	.986	.963	.989	.976	.991	.931	.970	.960	.985
Type III	.978	.988	.975	.988	.964	.982	.977	.990	.923	.973	.963	.984
Type IV	.975	.990	.974	.992	.979	.994	.976	.992	.949	.983	.971	.990
Ear height												
Type I	.974	.986	.976	.988	.970	.988	.976	.990	.928	.961	.965	.983
Type II	.964	.985	.959	.984	.960	.986	.967	.988	.928	.970	.956	.983
Type III	.973	.988	.955	.978	.967	.985	.964	.984	.955	.976	.963	.982
Type IV	.967	.987	.969	.989	.968	.990	.970	.987	.929	.976	.961	.986
Kernel row no.												
Type I	.958	.979	.967	.985	.949	.978	.949	.973	.952	.976	.955	.978
Type II	.886	.952	.876	.941	.894	.957	.816	.914	.787	.921	.852	.937
Type III	.889	.931	.914	.958	.901	.949	.805	.900	.732	.897	.848	.927
Type IV	.935	.977	.917	.979	.925	.987	.931	.973	.918	.977	.925	.979



Table 55. (Continued)

Character Type	Environment 1		Environment 2		Environment 3		Environment 4		Environment 5		Average	
	M1	M2	M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Ear length												
Type I	.958	.987	.955	.977	.937	.973	.959	.976	.933	.966	.948	.976
Type II	.920	.964	.909	.957	.886	.941	.931	.972	.897	.951	.909	.957
Type III	.931	.980	.953	.982	.914	.959	.930	.976	.887	.946	.923	.969
Type IV	.949	.979	.949	.982	.909	.974	.960	.988	.900	.957	.933	.976
Ear diameter												
Type I	.938	.969	.948	.987	.929	.973	.933	.971	.908	.956	.931	.971
Type II	.946	.981	.911	.981	.918	.978	.909	.963	.875	.960	.912	.973
Type III	.921	.961	.921	.977	.904	.969	.913	.963	.888	.954	.909	.965
Type IV	.918	.975	.902	.978	.917	.970	.934	.979	.900	.966	.914	.974
Yield												
Type I	.951	.973	.966	.983	.937	.967	.946	.967	.916	.958	.943	.970
Type II	.951	.982	.958	.985	.932	.966	.958	.979	.918	.970	.943	.976
Type III	.955	.984	.965	.985	.911	.971	.947	.976	.909	.955	.937	.974
Type IV	.951	.977	.957	.989	.962	.986	.963	.987	.916	.970	.950	.982
300-kernel wt.												
Type I	.879	.944	.900	.945	.859	.934	.906	.956	.883	.927	.875	.941
Type II	.892	.969	.919	.965	.944	.979	.897	.966	.908	.958	.912	.967
Type III	.878	.951	.916	.976	.935	.973	.863	.945	.889	.957	.896	.960
Type IV	.916	.969	.912	.970	.906	.953	.940	.975	.868	.961	.908	.964

Model 1 had better predictive value in Type I than Type II for plant height, ear height, kernel row number, ear length, and ear diameter. Model 1 had about equal predictive value for Types I and II with respect to yield. Comparing this with Model 2, Type I had higher correlations than Type II for kernel row number and ear length. Correlation coefficients for Model 2 were about equal for plant and ear height.

Type IV had better predictability than Type III by Model 1 for date silk, plant height, kernel row number, ear length and diameter, yield, and 300-kernel weight. Fitting Model 2 produced correlations that were higher for Type IV than Type III for all characters but date silk for which the correlation coefficients were practically equal.

It should be recalled that these correlations were calculated based on observed and predicted values in each particular environment. This will necessarily be different than fitting a common set of estimates to all environments. The correlations in the former case should be notably higher unless environmental effects were also fitted, which they were not.

Predictability was examined as the correlation of predicted values for Model 1 and Model 2, in one environment, with the observed values in another environment. Tables 56 through 63 give these correlations. Since date of silk was taken in only two environments, the information provided by this type of table was limited. For the other characters, the predictive value of Model 1 and Model 2, as regards other environments, was not clearly defined. When going from Model 1 to Model 2 the correlation coefficients went down as often as they went up. The two correlations were much closer to each other in these tables than when the predicted values

Table 56. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for date silk.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---					.916	.925		
	Env. 2			---	---						
	Env. 3					---	---				
	Env. 4	.918	.927					---	---		
	Env. 5									---	---
Type II	Env. 1	---	---					.900	.897		
	Env. 2			---	---						
	Env. 3					---	---				
	Env. 4	.917	.905					---	---		
	Env. 5									---	---
Type III	Env. 1	---	---					.928	.932		
	Env. 2			---	---						
	Env. 3					---	---				
	Env. 4	.945	.937					---	---		
	Env. 5									---	---
Type IV	Env. 1	---	---					.911	.909		
	Env. 2			---	---						
	Env. 3					---	---				
	Env. 4	.913	.912					---	---		
	Env. 5									---	---

Table 57. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for plant height.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.946	.948	.936	.932	.956	.956	.931	.919
	Env. 2	.953	.951	---	---	.919	.919	.958	.963	.927	.914
	Env. 3	.934	.932	.909	.916	---	---	.922	.928	.927	.918
	Env. 4	.960	.958	.955	.962	.929	.930	---	---	.933	.923
	Env. 5	.901	.902	.891	.894	.900	.900	.900	.903	---	---
Type II	Env. 1	---	---	.941	.946	.924	.930	.937	.944	.901	.895
	Env. 2	.942	.942	---	---	.931	.934	.920	.930	.891	.885
	Env. 3	.922	.929	.928	.937	---	---	.920	.927	.897	.891
	Env. 4	.948	.945	.929	.934	.932	.929	---	---	.917	.906
	Env. 5	.869	.877	.859	.871	.868	.874	.875	.887	---	---
Type III	Env. 1	---	---	.961	.955	.921	.911	.914	.909	.892	.880
	Env. 2	.959	.955	---	---	.936	.929	.901	.900	.879	.857
	Env. 3	.908	.905	.925	.923	---	---	.830	.832	.851	.831
	Env. 4	.914	.911	.902	.901	.841	.839	---	---	.884	.873
	Env. 5	.860	.866	.850	.844	.833	.824	.853	.858	---	---
Type IV	Env. 1	---	---	.963	.965	.942	.943	.953	.956	.926	.921
	Env. 2	.962	.968	---	---	.947	.954	.948	.958	.917	.919
	Env. 3	.946	.948	.952	.955	---	---	.925	.928	.901	.895
	Env. 4	.953	.957	.950	.957	.922	.925	---	---	.935	.933
	Env. 5	.901	.914	.893	.910	.873	.884	.910	.924	---	---

Table 58. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for ear height.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.963	.960	.936	.930	.962	.961	.911	.895
	Env. 2	.965	.962	---	---	.931	.926	.963	.962	.920	.902
	Env. 3	.931	.932	.924	.926	---	---	.921	.924	.915	.899
	Env. 4	.964	.965	.963	.964	.927	.925	---	---	.915	.898
	Env. 5	.867	.872	.874	.877	.875	.875	.870	.872	---	---
Type II	Env. 1	---	---	.904	.901	.910	.910	.929	.932	.881	.868
	Env. 2	.900	.901	---	---	.907	.912	.893	.897	.851	.834
	Env. 3	.906	.911	.907	.913	---	---	.898	.907	.907	.899
	Env. 4	.932	.935	.901	.900	.905	.909	---	---	.895	.885
	Env. 5	.848	.855	.824	.821	.877	.885	.859	.869	---	---
Type III	Env. 1	---	---	.941	.933	.900	.892	.943	.943	.875	.861
	Env. 2	.924	.924	---	---	.892	.888	.899	.908	.856	.843
	Env. 3	.895	.890	.903	.894	---	---	.853	.850	.877	.859
	Env. 4	.934	.939	.908	.914	.850	.849	---	---	.867	.860
	Env. 5	.859	.851	.857	.842	.866	.851	.860	.853	---	---
Type IV	Env. 1	---	---	.947	.951	.924	.924	.940	.947	.903	.896
	Env. 2	.949	.953	---	---	.940	.945	.921	.929	.894	.892
	Env. 3	.925	.927	.940	.947	---	---	.920	.922	.895	.884
	Env. 4	.944	.947	.922	.928	.922	.919	---	---	.928	.919
	Env. 5	.868	.885	.857	.881	.859	.871	.888	.909	---	---

Table 59. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for kernel row number.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.937	.930	.920	.905	.921	.905	.854	.833
	Env. 2	.946	.935	---	---	.931	.918	.935	.933	.855	.842
	Env. 3	.911	.904	.914	.912	---	---	.895	.886	.809	.794
	Env. 4	.912	.898	.917	.921	.895	.881	---	---	.877	.871
	Env. 5	.848	.830	.843	.835	.811	.792	.881	.874	---	---
Type II	Env. 1	---	---	.809	.817	.769	.775	.697	.693	.532	.523
	Env. 2	.799	.808	---	---	.809	.831	.663	.655	.460	.466
	Env. 3	.776	.779	.826	.845	---	---	.569	.576	.441	.467
	Env. 4	.641	.665	.618	.636	.519	.550	---	---	.485	.513
	Env. 5	.473	.506	.414	.456	.389	.450	.468	.517	---	---
Type III	Env. 1	---	---	.844	.830	.811	.781	.690	.675	.565	.505
	Env. 2	.868	.854	---	---	.831	.810	.691	.678	.531	.488
	Env. 3	.822	.796	.819	.802	---	---	.581	.570	.536	.450
	Env. 4	.624	.653	.609	.637	.519	.540	---	---	.452	.451
	Env. 5	.465	.486	.426	.457	.436	.425	.411	.449	---	---
Type IV	Env. 1	---	---	.896	.921	.902	.913	.903	.923	.868	.884
	Env. 2	.878	.923	---	---	.870	.909	.836	.862	.802	.842
	Env. 3	.891	.922	.877	.917	---	---	.869	.894	.861	.898
	Env. 4	.898	.920	.848	.857	.875	.882	---	---	.865	.880
	Env. 5	.851	.884	.803	.840	.854	.888	.853	.883	---	---

Table 60. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for ear length.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.922	.927	.847	.843	.920	.923	.874	.866
	Env. 2	.918	.918	---	---	.844	.823	.896	.896	.891	.876
	Env. 3	.829	.831	.828	.819	---	---	.846	.837	.789	.775
	Env. 4	.921	.913	.900	.895	.865	.840	---	---	.897	.874
	Env. 5	.851	.848	.871	.867	.785	.769	.873	.865	---	---
Type II	Env. 1	---	---	.877	.868	.734	.725	.837	.843	.765	.757
	Env. 2	.867	.862	---	---	.783	.777	.840	.853	.769	.747
	Env. 3	.706	.708	.763	.763	---	---	.739	.740	.665	.653
	Env. 4	.846	.850	.860	.866	.776	.765	---	---	.765	.749
	Env. 5	.746	.747	.759	.744	.674	.660	.737	.733	---	---
Type III	Env. 1	---	---	.881	.885	.720	.728	.871	.891	.750	.735
	Env. 2	.902	.886	---	---	.805	.804	.880	.874	.769	.751
	Env. 3	.707	.712	.772	.786	---	---	.742	.732	.640	.616
	Env. 4	.871	.881	.859	.870	.755	.745	---	---	.717	.722
	Env. 5	.715	.710	.716	.724	.621	.607	.684	.700	---	---
Type IV	Env. 1	---	---	.872	.867	.904	.895	.911	.921	.896	.874
	Env. 2	.872	.869	---	---	.868	.851	.894	.894	.891	.879
	Env. 3	.866	.890	.832	.843	---	---	.853	.885	.856	.867
	Env. 4	.922	.929	.905	.899	.901	.897	---	---	.911	.903
	Env. 5	.849	.854	.845	.856	.846	.852	.854	.857	---	---

Table 61. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for ear diameter.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.905	.904	.880	.862	.896	.874	.842	.829
	Env. 2	.914	.921	---	---	.874	.884	.892	.892	.880	.887
	Env. 3	.871	.865	.857	.871	---	---	.863	.848	.811	.798
	Env. 4	.891	.876	.879	.877	.868	.846	---	---	.844	.831
	Env. 5	.815	.817	.844	.858	.793	.784	.821	.818	---	---
Type II	Env. 1	---	---	.896	.877	.880	.864	.870	.855	.741	.717
	Env. 2	.862	.876	---	---	.874	.912	.853	.856	.776	.783
	Env. 3	.853	.861	.880	.909	---	---	.833	.819	.714	.722
	Env. 4	.836	.840	.851	.841	.825	.807	---	---	.786	.761
	Env. 5	.685	.702	.746	.767	.681	.709	.757	.759	---	---
Type III	Env. 1	---	---	.863	.857	.868	.861	.844	.815	.756	.730
	Env. 2	.863	.871	---	---	.870	.878	.850	.847	.809	.822
	Env. 3	.852	.868	.854	.871	---	---	.799	.799	.746	.733
	Env. 4	.837	.817	.842	.835	.807	.795	---	---	.816	.780
	Env. 5	.729	.724	.780	.803	.734	.722	.794	.773	---	---
Type IV	Env. 1	---	---	.859	.881	.863	.887	.877	.909	.850	.863
	Env. 2	.845	.884	---	---	.814	.840	.842	.880	.831	.866
	Env. 3	.863	.884	.827	.833	---	---	.881	.905	.835	.835
	Env. 4	.892	.913	.871	.880	.897	.914	---	---	.862	.876
	Env. 5	.834	.855	.829	.855	.819	.832	.831	.864	---	---



Table 62. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for yield.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.917	.912	.859	.855	.904	.884	.863	.844
	Env. 2	.930	.921	---	---	.876	.862	.907	.897	.882	.861
	Env. 3	.845	.849	.850	.848	---	---	.842	.823	.771	.742
	Env. 4	.899	.879	.889	.883	.850	.824	---	---	.866	.834
	Env. 5	.831	.830	.837	.839	.754	.734	.838	.826	---	---
Type II	Env. 1	---	---	.913	.911	.880	.869	.914	.925	.847	.824
	Env. 2	.921	.915	---	---	.922	.911	.921	.922	.855	.818
	Env. 3	.863	.854	.897	.892	---	---	.872	.874	.811	.786
	Env. 4	.921	.921	.921	.915	.896	.886	---	---	.870	.830
	Env. 5	.818	.813	.819	.805	.798	.790	.834	.823	---	---
Type III	Env. 1	---	---	.903	.897	.864	.854	.907	.891	.807	.786
	Env. 2	.912	.899	---	---	.881	.859	.905	.899	.853	.825
	Env. 3	.824	.843	.832	.847	---	---	.813	.801	.774	.738
	Env. 4	.899	.885	.888	.891	.844	.805	---	---	.839	.830
	Env. 5	.768	.763	.804	.800	.773	.726	.807	.812	---	---
Type IV	Env. 1	---	---	.893	.885	.886	.888	.923	.922	.908	.888
	Env. 2	.899	.897	---	---	.903	.910	.929	.931	.902	.881
	Env. 3	.897	.897	.907	.907	---	---	.904	.898	.869	.844
	Env. 4	.934	.932	.934	.929	.905	.899	---	---	.917	.896
	Env. 5	.875	.881	.863	.863	.827	.830	.872	.880	---	---

Table 63. Correlation of predicted values in one environment with observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types for 300-kernel weight.

Type	Observed values	Predicted values									
		Environment 1		Environment 2		Environment 3		Environment 4		Environment 5	
		M1	M2	M1	M2	M1	M2	M1	M2	M1	M2
Type I	Env. 1	---	---	.651	.642	.564	.509	.791	.787	.754	.729
	Env. 2	.667	.643	---	---	.668	.648	.557	.554	.693	.688
	Env. 3	.551	.504	.637	.640	---	---	.482	.465	.551	.543
	Env. 4	.816	.797	.560	.560	.508	.476	---	---	.800	.785
	Env. 5	.758	.715	.680	.674	.566	.539	.779	.761	---	---
Type II	Env. 1	---	---	.734	.719	.636	.633	.818	.833	.775	.764
	Env. 2	.756	.716	---	---	.822	.810	.787	.751	.760	.742
	Env. 3	.673	.640	.845	.821	---	---	.730	.711	.622	.609
	Env. 4	.823	.830	.769	.751	.694	.701	---	---	.785	.795
	Env. 5	.789	.755	.750	.736	.599	.595	.795	.788	---	---
Type III	Env. 1	---	---	.757	.776	.733	.738	.792	.799	.650	.661
	Env. 2	.790	.797	---	---	.820	.821	.793	.810	.618	.627
	Env. 3	.781	.755	.837	.819	---	---	.772	.752	.490	.493
	Env. 4	.779	.794	.747	.785	.713	.731	---	---	.669	.696
	Env. 5	.658	.665	.600	.614	.466	.484	.689	.704	---	---
Type IV	Env. 1	---	---	.777	.798	.751	.767	.824	.841	.791	.790
	Env. 2	.774	.799	---	---	.852	.877	.630	.654	.732	.742
	Env. 3	.742	.755	.846	.862	---	---	.597	.621	.653	.639
	Env. 4	.846	.846	.649	.657	.619	.635	---	---	.836	.812
	Env. 5	.749	.784	.696	.735	.625	.644	.772	.800	---	---

were compared in the same environment from which they were predicted. Kernel row number provided, by far, the most difference between Model 1 and Model 2 for prediction, being for the most part in favor of a higher value for Model 2. Environment 5 had the lowest correlations and was the hardest to predict from. The general level of correlation in these tables was lower, as expected, than the levels in the first set of correlation tables. Coefficients as low as 0.4 occurred occasionally, with many in the 0.7 and 0.8 ranges.

Complementing the previous correlations of predicted with observed in different environments were the correlations of observed in one environment with observed in another. Table 64 contains this information. In nearly all cases, the correlations of observed with observed in different environments, were higher for Types I and IV than Types II and III, respectively. Exceptions were Type I versus Type II in yield and 300-kernel weight, for which Type II showed the highest correlations.

Tables 56 through 63 were used to obtain the average correlation of predicted values from Model 1 or Model 2 in one environment with observed values in the other four environments. For example: the average correlation of predicted values from Model 1 in environment 1 with observed values in the other four environments was the average of four correlation coefficients. These four were the correlations of predicted values from Model 1 in environment 1 with observed values in environment 2, environment 3, environment 4, and environment 5. Table 64 provided a comparable value for the average correlation of observed with observed, e.g., the average correlation of observed values in environment 1 with observed values in the other four environments was calculated by averaging  $r_{12}$ ,  $r_{13}$ ,  $r_{14}$ , and  $r_{15}$ .

Table 64. Correlation of observed values with observed values by Types for the five environments.  
 (Note:  $r_{12}$  represents the correlation of observed in environment 1 with observed in  
 in environment 2, etc.)

Character Type	$r_{12}$	$r_{13}$	$r_{14}$	$r_{15}$	$r_{23}$	$r_{24}$	$r_{25}$	$r_{34}$	$r_{35}$	$r_{45}$
Date silk										
Type I			.921							
Type II			.894							
Type III			.919							
Type IV			.904							
Plant height										
Type I	.943	.929	.949	.899	.909	.955	.893	.923	.895	.900
Type II	.942	.927	.940	.872	.929	.926	.861	.926	.866	.888
Type III	.950	.901	.908	.858	.921	.899	.832	.829	.804	.858
Type IV	.962	.938	.954	.899	.951	.959	.906	.921	.880	.918
Ear height										
Type I	.951	.921	.953	.871	.915	.955	.874	.915	.867	.863
Type II	.891	.902	.925	.841	.903	.895	.805	.903	.881	.856
Type III	.927	.884	.933	.847	.886	.896	.831	.840	.842	.850
Type IV	.946	.916	.942	.869	.934	.927	.877	.913	.864	.902
Kernel row no.										
Type I	.915	.888	.879	.821	.902	.910	.833	.870	.785	.854
Type II	.765	.751	.645	.506	.799	.613	.440	.538	.465	.477
Type III	.825	.745	.617	.480	.782	.629	.451	.524	.408	.368
Type IV	.905	.910	.904	.867	.905	.842	.822	.877	.876	.875

Table 64. (Continued)

Character Type	r <sub>12</sub>	r <sub>13</sub>	r <sub>14</sub>	r <sub>15</sub>	r <sub>23</sub>	r <sub>24</sub>	r <sub>25</sub>	r <sub>34</sub>	r <sub>35</sub>	r <sub>45</sub>
Ear length										
Type I	.915	.826	.900	.843	.816	.887	.853	.817	.759	.860
Type II	.839	.685	.825	.734	.752	.841	.718	.735	.643	.708
Type III	.878	.709	.870	.700	.771	.856	.726	.716	.595	.695
Type IV	.855	.893	.921	.844	.841	.889	.849	.894	.841	.868
Ear diameter										
Type I	.907	.843	.863	.797	.868	.877	.853	.832	.773	.819
Type II	.854	.855	.830	.690	.896	.835	.761	.805	.710	.754
Type III	.847	.825	.787	.705	.838	.821	.788	.772	.706	.718
Type IV	.871	.872	.904	.841	.813	.868	.850	.901	.804	.857
Yield										
Type I	.904	.836	.859	.826	.843	.880	.830	.806	.721	.812
Type II	.903	.841	.908	.806	.888	.909	.789	.849	.761	.801
Type III	.880	.833	.874	.753	.831	.873	.796	.787	.718	.791
Type IV	.881	.883	.915	.869	.901	.921	.866	.898	.827	.874
300-kernel wt.										
Type I	.619	.516	.792	.697	.619	.548	.628	.490	.499	.750
Type II	.688	.609	.807	.727	.799	.723	.710	.689	.591	.770
Type III	.780	.722	.769	.633	.807	.771	.608	.725	.474	.661
Type IV	.795	.757	.836	.766	.858	.652	.732	.621	.630	.794

The result of this averaging was Table 65 which shows the average correlations of observed and predicted values in one environment with the observed values in the other four environments.

The average correlations were generally higher for predicted with observed than observed with observed. This was expected, since a better correspondence would be obtained when at least one member of each pair of values was predicted, and relative to other pairs would be more "in line". Correlations of predicted with predicted should be even higher. This result indicated a definite predictive value for Model 1 and Model 2. It was noted, however, that the relative value of Model 2 versus Model 1 was not clear from the figures. Table 65 also contains the mean of the average correlations of predicted values in one environment with observed in the others. In these, the Model 2 correlation was higher for the following: Type I for date silk, Type IV for plant height, Types II and IV for kernel row number, Type IV for ear length, Types II and IV for ear diameter, and Type III and IV for 300-kernel weight. Regardless of which Model correlation was highest, the greatest difference between the mean of the average correlations in any pair of Model 1 and Model 2 correlations was 0.027 (Type IV, 300-kernel weight). The rest of the differences were much smaller.

Table 65. Average correlation of observed and predicted values in one environment with the observed values in the remaining four environments for Model 1 (M1) and Model 2 (M2) by Types.

Character Type	Environment 1			Environment 2			Environment 3		
	Obs.	M1	M2	Obs.	M1	M2	Obs.	M1	M2
Date silk									
Type I	.921	.918	.927						
Type II	.894	.917	.905						
Type III	.919	.945	.937						
Type IV	.904	.913	.912						
Plant height									
Type I	.930	.937	.936	.925	.925	.930	.914	.921	.920
Type II	.920	.920	.923	.915	.939	.922	.912	.914	.917
Type III	.904	.910	.909	.901	.909	.906	.864	.883	.876
Type IV	.938	.941	.947	.935	.939	.947	.923	.921	.927
Ear height									
Type I	.924	.932	.933	.924	.931	.932	.905	.917	.914
Type II	.890	.897	.901	.873	.884	.884	.897	.900	.904
Type III	.888	.903	.901	.885	.902	.896	.863	.902	.870
Type IV	.918	.921	.928	.921	.917	.927	.907	.911	.915
Kernel row no.									
Type I	.878	.904	.892	.890	.903	.899	.861	.889	.874
Type II	.667	.672	.689	.654	.667	.689	.638	.621	.651
Type III	.667	.695	.697	.672	.675	.681	.615	.649	.639
Type IV	.897	.879	.912	.869	.856	.884	.893	.875	.898

Environment 4			Environment 5			Average	
Obs.	M1	M2	Obs.	M1	M2	M1	M2
.921	.916	.925				.917	.926
.894	.900	.897				.909	.901
.919	.928	.932				.937	.935
.904	.911	.909				.912	.911
.932	.934	.937	.897	.929	.919	.929	.928
.920	.913	.919	.872	.901	.894	.917	.915
.873	.875	.875	.838	.877	.860	.891	.885
.938	.934	.941	.901	.920	.917	.931	.936
.921	.929	.930	.869	.915	.899	.925	.922
.895	.895	.901	.846	.885	.871	.892	.892
.880	.889	.889	.843	.869	.856	.893	.882
.921	.917	.927	.870	.950	.898	.923	.919
.878	.908	.899	.823	.849	.835	.891	.880
.568	.599	.610	.472	.479	.492	.608	.626
.535	.593	.593	.427	.521	.473	.627	.617
.875	.865	.891	.861	.849	.876	.865	.892



Table 65. (Continued)

Character Type	Environment 1			Environment 2			Environment 3		
	Obs.	M1	M2	Obs.	M1	M2	Obs.	M1	M2
Ear length									
Type I	.871	.880	.877	.868	.880	.877	.805	.835	.819
Type II	.771	.791	.792	.787	.815	.810	.704	.742	.732
Type III	.789	.799	.799	.808	.807	.816	.698	.725	.721
Type IV	.878	.877	.885	.859	.863	.866	.867	.880	.874
Ear diameter									
Type I	.853	.873	.870	.876	.871	.880	.829	.854	.844
Type II	.807	.809	.820	.837	.843	.849	.817	.815	.823
Type III	.791	.820	.820	.823	.835	.841	.785	.820	.814
Type IV	.872	.859	.884	.851	.847	.862	.847	.848	.869
Yield									
Type I	.856	.876	.870	.864	.873	.871	.801	.835	.819
Type II	.865	.881	.876	.872	.887	.881	.835	.874	.864
Type III	.835	.851	.847	.845	.857	.859	.792	.841	.811
Type IV	.887	.901	.902	.892	.899	.896	.877	.880	.882
300-kernel wt.									
Type I	.656	.698	.665	.603	.632	.629	.531	.577	.543
Type II	.708	.760	.735	.730	.775	.757	.672	.688	.685
Type III	.726	.752	.753	.741	.735	.749	.682	.683	.693
Type IV	.789	.778	.796	.759	.742	.763	.717	.712	.731

Environment 4			Environment 5			Average	
Obs.	M1	M2	Obs.	M1	M2	M1	M2
.866	.884	.880	.829	.863	.848	.868	.864
.777	.788	.792	.701	.741	.727	.775	.771
.784	.794	.799	.679	.719	.706	.769	.768
.893	.878	.894	.851	.889	.881	.877	.880
.848	.868	.858	.811	.844	.836	.862	.858
.806	.828	.822	.729	.754	.746	.810	.812
.775	.822	.809	.729	.782	.766	.816	.810
.883	.858	.889	.838	.845	.860	.851	.873
.839	.873	.857	.797	.845	.820	.860	.847
.867	.885	.886	.789	.846	.815	.875	.864
.831	.858	.851	.765	.818	.795	.845	.833
.902	.907	.908	.859	.899	.877	.897	.893
.645	.652	.642	.643	.699	.686	.652	.633
.747	.783	.771	.699	.735	.727	.748	.735
.731	.761	.766	.594	.607	.619	.708	.716
.726	.706	.729	.731	.735	.746	.735	.753

## DISCUSSION

Inbred lines of maize were designated Type I (1<sup>st</sup> Cycle) or Type II (2<sup>nd</sup> Cycle) solely on the basis of the source from which they were selected. Other than viability as an inbred line, none of the quantitative attributes considered in this study had any bearing on selection of one line over another. Since Type II inbreds were selected from improved sources, it was expected that as inbreds per se, they would demonstrate a more favorable direction of expression for each character than the Type I inbreds. The expectation was borne out as seen in the midparent observed values in Table 10.

The exact opposite was true in the selection of Type III ("good") versus Type IV ("poor") inbred lines. Type III lines were supposed to have earlier maturity, shorter plant and ear height, more kernel rows, larger ears, higher yield, and heavier kernels. All of these criteria were fulfilled, except kernel weight, which was lighter for the Type III midparent average than for the Type IV. The F<sub>1</sub> average performance in a Type closely followed that of the midparent with respect to differences between Types.

The adequacy of the generation mean analysis, and the assumptions on which it was based, determine the validity of the results. Adequacy of the generation mean analysis to account for variability will be discussed later; however, the extremely high correlations between observed values and predicted values from either Model 1 or Model 2 should be kept in mind.

Within a particular cross, the assumptions of Anderson and Kempthorne (1954) were appropriate. These were: absence of multiple alleles, no linkage, no lethal genes, constant viability of all genotypes, and additive

environmental effects. Absence of multiple alleles within a particular cross was reasonable, since the inbred lines were maintained by ear-to-row selfing prior to seed production for this study. Admittedly, there were many crosses and many generations and the possibility of a mutation occurring was real. Multiple alleles were in all probability present, when the seven inbreds in a Type were considered. So long as the definitions of the effects in a given cross were based on only two sets of alleles, the pooling of net effects of crosses within a Type was valid. A method of correcting for parent designations as  $P_1$  or  $P_2$  is described later. With the correction, the average effect of a given inbred in the background of the other six inbreds could be discussed in a manner similar to general combining ability effects of the diallel. The purpose of this study was to contrast the net effects of a Type and not to examine the effects of crosses within a Type.

Hayman (1958) stated that the effect of linkage was to increase the deviations after fitting Model 2. Either trigenic or higher order epistasis could also cause a similar effect. Three more segregating generations ( $F_3$ ,  $BS_1$ ,  $BS_2$ ) were available in this study than were included in Gamble's (1962a, 1962b) study. Even so, linkage equilibrium was not probable, though its effect should be lessened with the added generations. Gamble (1962a) indicated that the bias was expected to be most for additive x additive and dominance x dominance effects. Effects, estimated free of linkage bias, were described by Hayman (1960) and Van der Veen (1959).

The presence of lethal genes would be minimized by the maintenance of the inbred lines by selfing. Closely related to lethality was constant viability of the genotypes. There were obvious differences in genotypes

under the stress of drought (environment 3) and moisture (environment 5). The plants survived, but viability includes production of enough seed to have descendents. Barren plants do not have descendents. Though there were some isolated cases of barrenness, viability was judged satisfactory in the overall study. A few chlorotic plants were noted among the inbred lines; however, they did not result in missing hills since they were either eliminated at or before thinning. This was the only indication of lethality detected and it was not judged serious.

Additivity of environmental effects was not realized. A review of the combined analyses (Tables 19 through 22) showed far too much interaction, particularly environments  $\times$   $a$  and  $d$ , to assume additivity. Bias due to these genotype  $\times$  environment interactions would be of unknown magnitude and direction for each parameter [Gamble (1962a)]. The pooled estimates combined over environments were expected to contain less of this bias than pooled estimates in each environment, due to some averaging of biases over environments.

Two models were tested in the generation mean analysis: Model 1 consisting of  $m$ ,  $a$ , and  $d$ ; and Model 2 consisting of  $m$ ,  $a$ ,  $d$ ,  $aa$ ,  $ad$ , and  $dd$ . In retrospect, a model containing only  $m$  and  $d$ , and one containing  $m$ ,  $a$ ,  $d$ , and  $dd$  would have been of interest. This being based on the relatively small contribution of  $a$  in the first case and of  $aa$  and  $ad$  in the second. A decision could be made on the mono- versus digenic model, as was the original intent.

No statistical comparisons of the correlation coefficients were made as it was felt the value of fitting the epistatic parameters could be judged from a practical standpoint without knowledge of the statistical

significance. Comparison of any two correlation coefficients ( $r$ ) could be accomplished by transformation to a  $Z$  variable equal to  $\frac{1}{2} \log_e \frac{1+r}{1-r}$  with a standard error of the difference as  $\left( \frac{2}{n-3} \right)^{1/2}$  where  $n = 189$ . Then, the probability is found in any table of  $N(0, 1)$  for the quantity  $\frac{(Z_1 - Z_2)}{SE(Z_1 - Z_2)}$ .

Correction of the cancellation of  $\hat{a}$  and  $\hat{ad}$  effects for a given inbred, due to designation of  $P_1$  and  $P_2$  as either plus or minus for  $\hat{a}$  and  $\hat{ad}$ , could be accomplished by the following scheme. Write out a  $7 \times 7$  table for the effects (either  $\hat{a}$  or  $\hat{ad}$ ), deleting the main diagonal. Leave all entries above the diagonal alone and multiply all entries below the diagonal by minus one. Row summing across the table and averaging will give the particular net effect corrected for parent designation for the given inbred.

The above scheme is applicable only for looking at the average effect of a particular inbred. No simple solution was apparent to handle the cancelling effects due to  $P_1$  and  $P_2$  designation in pooling  $\hat{a}$  and  $\hat{ad}$  over crosses in a Type. One possible method would be to rank the parents from high to low based on "average performance" and assign them numbers one through seven. Then, the lower numbered parent would always be  $P_1$  in the generation mean analysis and all  $\hat{a}$  and  $\hat{ad}$  effects would be positive. The problem, however, is what "average performance" should be based on. A difference in ranking among environments would cause trouble in analyzing each environment, since a different inbred of a given pair could be  $P_1$  in one environment and  $P_2$  in another. Alternatively, the analyses could be computed using one set of designations of  $P_1$  and  $P_2$  and then, before pooling the effects, ask if  $P_1 > P_2$  for that cross. If a "no" answer is obtained then multiply the  $\hat{a}$  and  $\hat{ad}$  by  $-1.0$ . Further complications occur for the

combined effects unless observed values are averaged before making the fit. Since the parents could be of different rankings in different environments, a change in  $P_1$  and  $P_2$  between environments for the combined analysis would be eliminating some true differences. It should be noted that this problem had no effect on the analysis as performed with respect to either the correlation or regression analyses, and applied only to  $\hat{a}$  and  $\hat{a}d$  testing when the effects were pooled. Counts of the occurrence of significance in a Type were not affected.

There was no consistent effect of missing plots noted. The environment with the most missing plots, environment 3, did not have smaller variances than the other environments. This possibility could have arisen, especially in the parental generation, due to using duplicated inbreds as sources of the missing plot values. The effective error mean squares of Table 7 showed the values of environment 3 to be intermediate.

Four decimals were carried throughout the analysis. Showing the effects with two decimal places was realistic considering accuracy of the measurements. Even two decimals was a compromise between significant digits and consistency across characters. Plant and ear height were measured roughly  $\pm 5$  cm from true height, due to sighting errors and measuring stick placement on the ground.

Date silk should have been accurate; however, differences did exist in what was considered to be a silked ear shoot. Kernel row number was exact, except on ears where uneven row alignment made counting either difficult or impossible. Errors in measuring ear length and diameter were on the order of  $\pm 0.2$  cm. Larger measuring errors could have occurred for ear length depending on how the shank was broken from the butt of the ear.

Yield weighing errors were  $\pm 1$  g, while 300-kernel weight measuring errors were  $\pm 0.1$  g. Machine counting errors could have occurred in counting out the 300-kernel samples. Less than two decimals would have been satisfactory for all but ear diameter, where even rounded to two decimals, some of the effects were 0.00.

While all of the foregoing summarizations have been based on Types, there was often wide variation within a Type. The variation was most evident in the effects from the analyses combined over environments. Epistatic values 3, 4, and up to 10 times the size of that effect for the rest of the crosses were found. A check of crosses having such values was made, and certain crosses were seen to appear rather consistently over the characters studied. By examination of the crosses in a Type, a qualitative determination was made as to whether it was a general effect of the inbred or the specific cross which was causing the outstanding effects. A cross was not included in this category unless it had one or more outstanding epistatic effects for at least three of the eight characters. In Type I, cross 5 (38-11 x I205) was outstanding in four of the eight characters. Crosses 69 (B38 x R177) and 77 (B44 x L289) of Type IV were the most notable of all; they showed very high epistasis for seven and five characters, respectively. Within Type II there were several crosses showing high epistatic values, but when the inbreds in the crosses were examined, three were in common: A619, B14, and B55. The crosses in Type II did not show as high epistatic values as did the previously enumerated crosses of Types I and IV; hence, a general effect of the particular inbred.

The estimates of genetic effects combined over environments were in good agreement with those of Gamble (1962a, 1962b). Gamble's  $\hat{d}$ 's for yield



were relatively greater compared to  $\hat{m}$  than were those of this study. For yield, Gamble found 7 of 15 crosses significant for  $\hat{a}$ , while this study showed an average of 7 of 21 for Model 2 and 14 of 21 for Model 1. Gamble did not differentiate between Model 1 and Model 2 in his analysis, and all his statements pertaining to significant  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$  were based on Model 2, which according to Hayman (1960) was improper since the estimates of  $m$ ,  $a$ , and  $d$  were either biased in the presence of significant epistasis, or were estimated from the wrong equations if epistasis was not significant.

In view of this, the direction of change in  $\hat{m}$ ,  $\hat{a}$ , and  $\hat{d}$  was examined for Model 1 and Model 2. For all characters, the estimates of  $m$  remained practically the same, with a maximum change of about 2%. Estimates of  $a$  usually went up and down from Model 1 to Model 2, with the majority of changes being for a higher  $|\hat{a}|$  in most characters. Although the value of  $\hat{a}$  changes was generally up in absolute value, the occurrence of significance consistently decreased from Model 1 to Model 2. The reason for the decrease was the relative change of the  $c_{kk}$  term from the inverse matrix, and the lower margin by which  $\hat{a}$  was significant compared to  $\hat{m}$  and  $\hat{d}$ . The estimates of  $d$  increased substantially from Model 1 to Model 2 for yield and 300-kernel weight; increased slightly for ear height; and decreased slightly for date silk (more negative), kernel row number, and ear diameter. Other characters, and many crosses in the characters just mentioned, moved up or down with no net effect for all crosses. Since nearly all estimates of  $d$  were highly significant, no changes occurred except in magnitude of the effect. For 300-kernel weight, however, there was a decrease in significance of  $\hat{d}$  when considering Model 2 versus Model 1.

Date silk behaved differently than the other characters with respect

to epistasis. All the analyses of variance for date silk demonstrated more epistasis in Types I and III than in Types II and IV. The reason for this was not clear. The range of maturity from midparent to  $F_1$  was approximately the same for both pairs of Types. Therefore, the difference must have lain in the rates of inbreeding depression, i.e., the early segregating generations of Types I and III did not suffer much depression, whereas, Types II and IV did. The depression seen in Types II and IV was adequately described by the dominance effects, while epistasis was required to describe the slower rate of inbreeding depression in the early generations of Type I and III crosses.

When the relative rates of occurrence of significant epistasis were compared in the combined versus uncombined analyses of variance, more epistasis was present in the combined analyses. Type I for date silk, ear length, and yield had relatively fewer instances of significant epistasis in the combined analyses. Other character-Type combinations had increases of zero to nearly four times when comparing uncombined with combined analyses. Partitioning of the sums of squares into main effects and interactions was the cause. Since the epistatic interaction term was generally nonsignificant, removing degrees of freedom from the mean square's denominator, without removing a significant sum of squares for interactions in the numerator, caused a relatively larger main effect, or significant epistasis.

The analyses of variance for yield were in agreement on epistasis for Types I and II, but suggested a decrease in the relative difference between Types III and IV in going to the combined analyses. A distinct difference was apparent when the occurrences of significance in each environment were

summed; 14 for Type III versus 24 for Type IV. This was reduced to six versus seven, or on a five environment basis, 30 versus 35 in the combined analysis for Types III and IV. The pooled mean squares for epistasis from the combined analyses (Table 29) showed the pooled mean squares for Type IV to be nearly twice as large as those for Type III. In part this could be accounted for by a few large mean squares as occurred in the outstanding crosses previously described (cross numbers 69, 77, and 83). The mean square for epistasis in cross 69 was nearly 10 times larger than the pooled mean square. The cause of this was that R177, one of the parent lines, had poor silk emergence for pollination, resulting in much barrenness and very low plot yields. The large parental difference and relatively high yield of the  $F_1$  contributed to extremely high epistasis. The yield of many of the Type IV crosses fell off sharply from the  $F_3$  and backcrosses selfed ( $BS_1$  and  $BS_2$ ) to the parents. Thus, the pooled mean squares and effects could be greatly influenced by a relatively few crosses.

As for the decreased epistasis between Types III and IV in the combined analysis, this was due to the partitioning effect of removing a highly significant epistatic interaction sum of squares in five of the Type IV crosses, while none of the epistatic interactions were significant in Type III.

Considering the regression analyses, four things were evident. First, epistasis was of statistical significance for at least one of the 21 crosses for all characters. The importance varied widely from Type to Type and from character to character. Types II and IV showed higher levels of epistasis than Types I and III, respectively. Second, significant deviations due to higher order epistasis and(or) linkage, while of lesser frequency

than epistasis, were nonetheless important. They generally occurred at either half or less than half the frequency of epistasis. Considering the relatively small increase in sums of squares accounted for by fitting the digenic model after the monogenic model, it was likely that linkages were more important than higher order epistasis.

The occurrence of significant environments  $\times$  a and d interaction was the third item much in evidence. The frequency roughly paralleled that of epistasis but sometimes, such as with yield, there were very wide differences. Interactions, generally, arise either from a change in rank or an unequal response with no change in rank. The former explanation was preferred in this case. Even within Types, there was a wide range in material; hence, different responses to the environments were to be expected. The existence of these nonadditive responses to environments would question the assumption of environmental additivity used in many other studies. There were also implications regarding predictive value of the models in the presence of such extensive interactions. These were better demonstrated in the correlation analyses, which are discussed later.

The fourth and last observation related to the existence of significant interactions of environments  $\times$  epistasis and environments  $\times$  deviations from Model 2. Overall, these were of low incidence, except in Type I for plant height, ear length, and ear diameter. A high interaction could have shown up as significant epistasis and(or) deviations in the analyses conducted in each environment.

The interpretation of the genetic effects presented a problem in deciding what to use as a base. Picking one or more of the generations was not adequate.  $\hat{m}$  alone was not sufficient, nor was simply summing all

effects for all generations. While the  $F_2$  mean is defined as  $m$ , it contains all of the genetic effects included in the models. Estimates of the effects were obtained by differences in certain generations through least squares. The only suitable solution was to work with all the effects, keeping in mind the maximum coefficient that any effect could have. These maximums for the generations studied were 1, 1,  $\frac{1}{2}$ , 1, 1, and  $\frac{1}{4}$  for  $\hat{m}$ ,  $\hat{a}$ ,  $\hat{d}$ ,  $\hat{aa}$ ,  $\hat{ad}$ , and  $\hat{dd}$ , respectively.

Any significance for a given effect must be compared with the relative magnitude of the contribution with respect to  $\hat{m}$ . Due to size of the study and resulting diminution of errors by combining and pooling effects, statistical significance was obtained in some cases where practical significance was not. A good example was the effects for Type I plant height combined over environments and pooled over the 21 crosses. The estimate of  $m$  was about 200, while the highly significant estimate of  $aa$  was 2.46. At most, the contribution of the significant epistatic effect was barely over 1%, and not of practical significance.

The size of the  $\hat{d}$  and  $\hat{dd}$  genetic effects was associated with the degree of inbreeding depression as given in Table 10. Larger absolute values of  $\hat{d}$  and  $\hat{dd}$  occurred with those characters, such as yield and ear height, which showed the most effects of inbreeding.

Individual genetic effects in the combined analyses were viewed to obtain a general description of how the effects compared with respect to sign regardless of significance. Differences between Types did exist and the more outstanding of these were singled out. The estimates of  $d$  were negative in all crosses for date silk and a majority of the  $\hat{dd}$  effects were positive. The remaining effects were both positive and negative.

Plant and ear height had positive  $\hat{d}$  effects, while most of the estimates of  $dd$  were negative. Type II for both characters showed more negative contributions for  $\hat{a}$ ,  $\hat{aa}$ , and  $\hat{ad}$ . Types I, III, and IV for plant height were positive and negative in the estimates of  $a$ ,  $aa$ , and  $ad$ , except for the estimates of  $a$  in Type III, which were mostly negative. Type III estimates of  $aa$  and  $ad$  for ear height were generally positive, while Types I and II had more negative estimates of  $ad$ . Other effects for ear height were equally signed.

All estimates of  $d$  for kernel row number were positive. Most of the signs on  $\hat{dd}$  were negative. Estimates of  $a$  were more frequently positive in Types III and IV than Types I and II. Types II and IV had a preponderance of negative estimates for  $aa$ .

$\hat{d}$  and  $\hat{dd}$  effects were positive and negative, respectively, for ear length and diameter.  $\hat{aa}$  effects had a tendency to be negative in Types I and IV and positive in Types II and III. Type III had a very large number of negative estimates of  $a$  for ear diameter.

As for previous characters, except date silk, yield was positive for  $\hat{d}$  in all crosses and a majority of the crosses were negative for  $\hat{dd}$ . All estimates of  $aa$  in Type II were positive, while most of the estimates were positive in Types III and IV.  $\hat{a}$  was equally signed in Types I and II, positive in Type III, and negative in Type IV.  $\hat{ad}$  effects were of both signs in all but Type II, where negative signs predominated.

300-kernel weight estimates of  $d$  were positive for Types I and II, mostly positive for Type III, and equally signed in Type IV.  $\hat{dd}$  was negative in more than half of the crosses for only Types I and IV.  $\hat{aa}$  had a plus sign more frequently in Types II, III, and IV.  $\hat{a}$  and  $\hat{ad}$  were equally

positive and negative in Types I and IV, but generally positive in Type II and negative in Type III.

Agreement between the results of the regression analysis and the results of testing individual effects was examined. In this, the number of cases of significance in the combined analyses of variance (Tables 19 through 22) was compared to the frequency of significance of combined effects (Tables 48 through 51), using the 5% level of significance. Comparison of these results was limited to epistasis, since the large dominance contribution caused significance in the reduction of sum of squares due to  $a$  and  $d$  in nearly all cases, except date silk and 300-kernel weight. Date silk showed nearly equal reductions due to  $a$  and  $d$  for Types I and II, and a very slight increase in significance of Type III over Type IV. Individual combined effects were all significant for  $\hat{d}$ . For  $\hat{a}$ , Types I and II were equal and Type III had distinctly more cases of significance than Type IV. 300-kernel weight was simpler to compare for  $\hat{a}$  and  $\hat{d}$ . The regression analyses indicated Types II and III had, respectively, more cases of significant  $a$  and  $d$  sum of squares reduction than Types I and IV. Similarly, Types II and III showed more total cases of significance for  $\hat{a}$  and  $\hat{d}$  effects, than Types I and IV. For convenience, the tests of individual genetic effects will be referred to as "effect tests" in the following discussion.

More epistasis for date silk in the regression analyses was demonstrated by the crosses of Types I and III than II and IV. The margin was less in the difference between Types III and IV. Effects tests of epistasis showed 21 total incidences of significant epistasis in Type I versus six in Type II and 14 in Type III as opposed to only five in Type IV.

The distinction between Types I and II for plant height in the regression analyses was slight, but was in favor of more epistasis in Type II. Type IV had more than twice the occurrences of significant reduction due to epistasis than Type III. Effect tests totaled 24 cases of epistasis in Type I, 23 in Type II, 10 in Type III, and 27 in Type IV. The second comparison matched perfectly and the first was acceptable. A difference of two or three crosses was less meaningful when the total number of significant crosses was above 11 or 12 than when the total was less, i.e., a relative difference versus absolute.

The regression results for ear height suggested similar amounts of epistatic significance in Types I and II. Type III had considerably less epistasis than Type IV. Effect tests also showed Types I and II to be similar; 22 versus 20 cases of significant epistasis. Type III had 12 total instances of significant epistasis and Type IV had 22, which agreed very well with the regression results.

Kernel row number was very clear in its distinction between Types I and II and between Types III and IV. The number of times significant epistasis was noted in the regression results for Types II and IV was just about twice what was noted for Types I and III, respectively. The distinction was even greater in the effect tests. Type II had 14 cases of significance versus six for Type I and Type IV had 28 versus nine for Type III.

Regression results for ear length again showed more epistasis in Types II and IV than Types I and III. The difference was relatively greater between Types I and II. Type II effect tests resulted in 26 instances of significant epistatic effects as opposed to 14 for Type I. Type IV had 24, while Type III had 16. The order and relative differences are in concor-



- dance.

Types II and IV had more cases of significant epistasis in the regression analyses for ear diameter than did Types I and III. Type II minus Type I equaled three and Type IV minus Type III equaled eight. The differences found by effect tests were four and 14, respectively, for the two comparisons.

Yield had five times more cases of significant epistasis in Type II than Type I, according to regression analysis. The comparison of Types III and IV found a difference of only one cross, that, in favor of Type IV. Twenty-seven instances of significant epistatic effects were counted in Type II and eight in Type I, a decisive margin. Type III had 20 occurrences of significant epistatic effects, while Type IV had 18. Both methods of analysis show equal amounts of epistasis between Types III and IV for yield.

Equal 300-kernel weight epistasis was found by the regression analyses between Types I and II and between Types III and IV, but there were more than twice as many crosses having significant reduction due to epistasis in the latter comparison. Effect tests tallied up to nine cases of significant effects in Type I, 17 in Type II, 17 in Type III, and 22 in Type IV. This was the poorest agreement for any character. The primary contributor of more significance in Types II and IV was a consistently large  $\hat{a}a$  effect in most environments. Interactions did not appear frequently enough to have a bearing on the problem and no entirely satisfactory explanation was found.

Overall, the foregoing discussion indicated Type II and Type IV inbreds to have more epistatic gene action detectable than Types I and III. This is a reasonable division of the four Types. Type II inbreds were

selected from specific outstanding crosses and were more likely to have specific favorable epistatic and dominance relations selected. Type IV inbreds, as a class, were very good in specific combinations versus the general performance of the Type III inbreds; hence, a more specific non-additive reaction.

Characters which showed the most epistasis were plant height, ear height, kernel row number, and ear diameter. The lowest level of epistasis was demonstrated by date silk and the next lowest by yield. Any conclusion made with respect to yield must include the fact that yield had the highest environment x generation interaction of all characters.

Relating the results from regression analyses and effect tests with the results from correlation analyses, one would expect characters which showed high epistasis to have the greater changes in correlation coefficients from Model 1 to Model 2. Basically, this was true. Date silk and yield had relatively smaller average changes and kernel row number and ear diameter had relatively larger changes in fitting Model 2 over Model 1 (Table 52). Plant height and ear height did not conform to this expectation; the average correlations from fitting Model 1 were highest (0.96) of all characters. At this level of correlation, any large improvement in fit would be difficult. This relates again to the example of statistical significance versus practical significance. In spite of significant statistical epistasis, the initial fit by Model 1 was so good that little improvement could be made by fitting Model 2.

The correlation analyses related predicted and observed values in one environment with respect to importance of epistasis. The results for epistasis, from regression and effect tests, were based on combined analyses

and effects, respectively. No direct comparison of observed and predicted values based on combined effects was calculated. Average predictive values of the models were calculated. These results (Table 65) indicated an averaging of epistatic effects and(or) interactions with the environments, such that no additional information was obtained by fitting the epistatic components. Thus, a descriptive value in a given environment was realized by fitting the epistatic components, but a predictive value was not realized. If prediction was the primary aim, more gain would be made by using only the  $P_1$ ,  $P_2$ , and  $F_1$  generations and utilizing more environments. No additional information would be provided by the remaining generations if only Model 1 were to be estimated.

In terms of prediction, it must be noted that the generation mean model did not lead to a general predictive formulation for genetic gain, such as the heritability coefficient derived from the ratio of additive genetic variance to total variance. There was much intuitive appeal to the generation mean model, however, especially regarding the lower variances obtained on first order estimates. Variance analyses could only explain variation, where the generation mean analyses gave the genetic structure of the observation itself.

Disagreement was found in this study and those of Chi (1965) and Wright (1966). Both of the earlier studies had concluded that  $\sigma_A^2$  comprised the majority of the genetic variance present, or was very important. In this study additive effects were of lesser statistical significance than dominance effects and of much less importance in magnitude of contributions. The logical reason to explain the difference was the nature of the material studied. Both Chi and Wright used open-pollinated varieties and the lines

derived from those varieties were unselected. The inbreds in this study were, at the least, very highly selected. As a result, dominance effects were present in most crosses and characters to an extent that the additive effects were small by comparison. In a similar manner, the additional selection which occurred in Type II inbreds of this study resulted in more epistasis than the Type I inbreds.

Implications regarding breeding procedures follow from the above observations. Open-pollinated varieties showed a preponderance of additive variation [Chi (1965) and Wright (1966)]. Inbreds isolated from the open-pollinated varieties (Type I) with selection, demonstrated more nonadditive gene action, particularly dominance effects, than was found in the open-pollinated varieties. Inbreds isolated from recombination of choice lines (Type II) and subjected to further selection, showed more epistatic effects than Type I inbreds. The good inbreds of this study (Type III) were good as inbreds because of additive effects and some degree of additive x additive epistasis, since neither dominance, additive x dominance, or dominance x dominance effects could occur in a homozygous line. The poor inbreds (Type IV) were lacking in the additive effects of Type III but were highly responsive to heterozygosity in the way of nonadditive gene action.

F<sub>1</sub> average yields were higher for Types II and IV than Types I and III (Table 10). Based on this sample of lines, a procedure which would detect and select favorable nonadditive gene action, i.e., dominance and epistasis, should result in better performance if highly heterozygous plants are to be grown. Interaction with environments was indicated to be more important with the more highly specific lines, e.g., Type IV inbreds.

## SUMMARY

The objective of this study was to estimate and compare the genetic effects of four Types of maize inbreds. The first comparison was to be made between 1<sup>st</sup> Cycle (Type I) inbreds which had been isolated from open-pollinated varieties and 2<sup>nd</sup> Cycle (Type II) inbreds selected from segregates of planned crosses or synthetic varieties. The second comparison was between good (Type III) and poor (Type IV) inbreds per se. Seven inbreds of each Type were selected and all possible F<sub>1</sub>'s, F<sub>2</sub>'s, F<sub>3</sub>'s, backcrosses, and backcrosses selfed were made within a Type.

Second Cycle inbreds, as opposed to 1<sup>st</sup> Cycle inbreds, had earlier maturity, shorter plants, more kernel rows, larger ears, higher yields, and heavier kernels. Good versus poor inbreds were in the same relation as 2<sup>nd</sup> Cycle versus 1<sup>st</sup> Cycle inbreds, except that the poor inbreds had heavier kernels than the good inbreds.

Hayman's (1958) generation mean analysis, as modified by Gamble (1962a), was used to estimate the genetic effects. Nine generations from each cross were included: parents (P<sub>1</sub> and P<sub>2</sub>), F<sub>1</sub>, F<sub>2</sub>, F<sub>3</sub>, backcrosses to both parents (BC<sub>1</sub> and BC<sub>2</sub>), and the backcrosses selfed (BS<sub>1</sub> and BS<sub>2</sub>).

Data were obtained in five random environments for seven quantitative characters: plant height, ear height, kernel row number, ear length, ear diameter, yield, and 300-kernel weight. Date of silk data were taken in two of the five environments. A simple rectangular lattice (SRL) analysis of variance was performed on each generation in each environment. The adjusted means from the SRL analyses were used as the input for the generation mean analyses.

Two genetic models were fitted by unweighted least squares. Model 1 consisted of:  $m$ , due to mean genetic effects;  $a$ , due to additive genetic effects; and  $d$ , due to dominance genetic effects. Model 2 consisted of Model 1 plus the digenic epistatic effects:  $aa$ , due to additive x additive genetic effects;  $ad$ , due to additive x dominance genetic effects; and  $dd$ , due to dominance x dominance genetic effects. Regression analyses were combined over environments providing information on the importance of environment x genetic effect interactions. Individual genetic effects were tested for significance; and differences of effects were compared between 1<sup>st</sup> and 2<sup>nd</sup> Cycle inbreds and between good and poor inbreds. Observed and predicted values were correlated within and across environments.

Dominance effects were larger and more significant than additive effects for all characters, except kernel row number and 300-kernel weight. For these two characters, dominance effects showed more statistical significance, but the contributions of additive and dominance effects were nearly equivalent.

Epistasis was found to be significant in at least one cross in each Type for each character. The importance of epistasis varied among characters, being least important for date silk and yield and most important for plant height, ear height, and ear diameter. Epistasis for date silk was more important in 1<sup>st</sup> Cycle and good inbreds than 2<sup>nd</sup> Cycle and poor inbreds. For plant and ear height, kernel row number, ear length, and ear diameter, the 2<sup>nd</sup> Cycle and poor inbreds showed more epistasis than the 1<sup>st</sup> Cycle and good inbreds, respectively. For yield, the 2<sup>nd</sup> Cycle inbreds demonstrated far more epistasis than the 1<sup>st</sup> Cycle inbreds. Good and poor inbreds showed little difference in the occurrence of significant epistasis

for yield. The epistatic differences between 1<sup>st</sup> Cycle and 2<sup>nd</sup> Cycle inbreds and between good and poor inbreds were negligible for 300-kernel weight.

Deviations from Model 2 were of less importance than epistasis, but still frequent enough to be considered as having a significant contribution. Linkage was discussed as a likely source of these deviations, versus tri-genic or higher order epistasis.

Environmental interactions with additive and dominance effects were important for all characters, especially yield. Interaction of environments x epistasis was of low frequency, except for yield in the crosses of poor inbreds.

Correlations of observed values with predicted values in each environment from Model 1 and Model 2 indicated a gain in information by fitting the epistatic parameters. For date silk, plant height, ear height, and yield the gain was relatively small since the correlations averaged over environments using Model 1 were all above 0.93.

Prediction of an arbitrary environment was investigated by computing the correlations of predicted values in one environment with observed values in another environment. The results indicated that a monogenic model was adequate for prediction.

## LITERATURE CITED

- Anderson, V. L. 1953. A model for the study of quantitative inheritance. Unpublished Ph.D. thesis. Library, Iowa State University of Science and Technology, Ames, Iowa.
- Anderson, V. L., and O. Kempthorne. 1954. A model for the study of quantitative inheritance. *Genetics* 39:883-898.
- Bauman, L. F. 1959. Evidence of non-allelic gene interaction in determining yield, ear height, and kernel row number in corn. *Agron. J.* 51:531-534.
- Chi, K. 1965. Covariances among relatives in a random mating population of maize. Unpublished Ph.D. thesis. Library, Iowa State University of Science and Technology, Ames, Iowa.
- Cochran, W. G., and G. M. Cox. 1968. *Experimental designs*. 2nd ed. John Wiley & Sons, Inc., New York, New York.
- Cockerham, C. C. 1954. An extension of the concept of partitioning hereditary variance for analysis of covariance among relatives when epistasis is present. *Genetics* 39:859-882.
- Cockerham, C. C. 1956a. Analysis of quantitative gene action. *Brookhaven Symposia of Biology* 9:53-68.
- Cockerham, C. C. 1956b. Effects of linkage on the covariances between relatives. *Genetics* 41:138-141.
- Comstock, R. E., and H. F. Robinson. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. *Biometrics* 4:254-266.
- Eberhart, S. A., and C. O. Gardner. 1966. A general model for genetic effects. *Biometrics* 22:864-881.
- Eberhart, S. A., R. H. Moll, H. F. Robinson, and C. C. Cockerham. 1966. Epistatic and other genetic variances in two varieties of maize. *Crop Sci.* 6:275-280.
- Eberhart, S. A., W. A. Russell, and L. H. Penny. 1964. Double cross hybrid prediction in maize when epistasis is present. *Crop Sci.* 4:363-366.
- Fisher, R. A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Trans. Royal Soc. Edinburgh* 52:399-433.



- Fisher, R. A., F. R. Immer, and O. Tedin. 1932. The genetical interpretation of statistics of the third degree in the study of quantitative inheritance. *Genetics* 17:107-124.
- Gamble, E. E. 1957. Relative importance of epistatic and nonepistatic gene effects in maize. Unpublished Ph.D. thesis. Library, Iowa State University of Science and Technology, Ames, Iowa.
- Gamble, E. E. 1962a. Gene effects in corn (Zea mays L.). I. Separation and relative importance of gene effects for yield. *Can. J. Pl. Sci.* 42:339-348.
- Gamble, E. E. 1962b. Gene effects in corn (Zea mays L.). II. Relative importance of gene effects for plant height and certain component attributes of yield. *Can. J. Pl. Sci.* 42:349-358.
- Gardner, C. O., and S. A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. *Biometrics* 22:439-452.
- Gorsline, G. W. 1961. Phenotype epistasis for ten quantitative characters in maize. *Crop Sci.* 1:55-58.
- Hayman, B. I. 1954. Theory and analysis of diallel crosses. *Genetics* 39:789-809.
- Hayman, B. I. 1957. Interaction, heterosis, and diallel crosses. *Genetics* 42:336-355.
- Hayman, B. I. 1958. The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12:371-390.
- Hayman, B. I. 1960. The separation of epistatic from additive and dominance variation in generation means. II. *Genetica* 31:133-146.
- Hayman, B. I., and K. Mather. 1955. The description of genetic interaction in continuous variation. *Biometrics* 11:69-82.
- Henderson, C. B. 1964. Inbred lines of corn released to private growers from state and federal agencies and lists of double crosses by states. 4th revision. Illinois Seed Producers' Association, Champaign, Illinois.
- Hull, F. H. 1945. Recurrent selection for specific combining ability in corn. *J. Am. Soc. Agron.* 37:134-145.
- Jinks, J. L. 1954. The analysis of heritable variation in a diallel cross of Nicotiana rustica varieties. *Genetics* 39:767-788.
- Jinks, J. L. 1955. A survey of the genetical basis of heterosis in a variety of diallel crosses. *Heredity* 9:223-238.

- Jinks, J. L. 1956. The  $F_2$  and backcross generations from a set of diallel crosses. *Heredity* 10:1-30.
- Jinks, J. L., and R. M. Jones. 1958. Estimation of components of heterosis. *Genetics* 43:223-234.
- Kempthorne, O. 1957. An introduction to genetic statistics. John Wiley & Sons, Inc., New York, New York.
- Kinman, M. L., and G. F. Sprague. 1945. Relation between number of parental lines and theoretical performance of synthetic varieties of corn. *J. Am. Soc. Agron.* 37:341-351.
- Mather, K. 1949. Biometrical genetics. Methuen & Co. Ltd., London, England.
- Robinson, H. F., and R. E. Comstock. 1955. Analysis of genetic variability in corn with reference to probable effects of selection. *Cold Spring Harbor Symposia on Quant. Biol.* 20:127-135.
- Robinson, H. F., R. E. Comstock, and P. H. Harvey. 1949. Estimates of heritability and the degree of dominance in corn. *Agron. J.* 41:353-359.
- Robinson, H. F., and G. S. Watson. 1949. An analysis of simple and triple rectangular lattice designs. *North Carolina Agr. Expt. Sta. Tech. Bul.* 88.
- Schnell, F. W. 1963. The covariance between relatives in the presence of linkage. In Hanson and Robinson, eds. *Statistical genetics and plant breeding*. Nat. Acad. Sci.-Nat. Res. Council Pub. 982.
- Sprague, G. F. 1955. Problems in the estimation and utilization of genetic variability. *Cold Spring Harbor Symposia on Quant. Biol.* 20:87-92.
- Sprague, G. F., W. A. Russell, L. H. Penny, T. W. Horner, and W. D. Hanson. 1962. Effect of epistasis on grain yield in maize. *Crop Sci.* 2:205-208.
- Thompson, D. L., J. O. Rawlings, and R. H. Moll. 1963. Inheritance and breeding information pertaining to brown spot resistance in corn. *Crop Sci.* 3:511-514.
- Van der Veen, J. H. 1959. Tests of non-allelic interaction and linkage for quantitative characters in generations derived from two diploid lines. *Genetica* 30:201-232.
- Wright, J. A. 1966. Estimation of components of genetic variance in an open-pollinated variety of maize using single and three-way crosses among random inbred lines. Unpublished Ph.D. thesis. Library, Iowa State University of Science and Technology, Ames, Iowa.

## ACKNOWLEDGEMENTS

I wish to extend my appreciation to Dr. Arnel R. Hallauer for his contribution to this study and my graduate program. In addition, thanks are due Drs. S. A. Eberhart, L. H. Penny, and W. A. Russell for their encouragement and assistance. The study could not have been undertaken without the aid of the Corn Breeding Technicians and their efforts in accomplishing the field work are commended.

I thank my wife, Bonnie, for her patience with me and for typing the final manuscript.

APPENDIX

Table 66. Listing of  $F_1$  crosses by Types.

Type I		Type II	
Cross no.	Cross	Cross no.	Cross
1	38-11 x WF9	22	A619 x B14
2	38-11 x Hy	23	A619 x B37
3	38-11 x L317	24	A619 x (B38 x B217)Selected
4	38-11 x L289	25	A619 x B50
5	38-11 x I205	26	A619 x B54
6	38-11 x I159	27	A619 x B55
7	WF9 x Hy	28	B14 x B37
8	WF9 x L317	29	B14 x (B38 x B217)Selected
9	WF9 x L289	30	B14 x B50
10	WF9 x I205	31	B14 x B54
11	WF9 x I159	32	B14 x B55
12	Hy x L317	33	B37 x (B38 x B217)Selected
13	Hy x L289	34	B37 x B50
14	Hy x I205	35	B37 x B54
15	Hy x I159	36	B37 x B55
16	L317 x L289	37	(B38 x B217)Selected x B50
17	L317 x I205	38	(B38 x B217)Selected x B54
18	L317 x I159	39	(B38 x B217)Selected x B55
19	L289 x I205	40	B50 x B54
20	L289 x I159	41	B50 x B55
21	I205 x I159	42	B54 x B55

Table 66. (Continued)

Type III		Type IV	
Cross no.	Cross	Cross no.	Cross
43	B46 x B50	64	B38 x B39
44	B46 x B53	65	B38 x B44
45	B46 x B55	66	B38 x B52
46	B46 x B57	67	B38 x B54
47	B46 x A619	68	B38 x L289
48	B46 x (B38 x B217)Selected	69	B38 x R177
49	B50 x B53	70	B39 x B44
50	B50 x B55	71	B39 x B52
51	B50 x B57	72	B39 x B54
52	B50 x A619	73	B39 x L289
53	B50 x (B38 x B217)Selected	74	B39 x R177
54	B53 x B55	75	B44 x B52
55	B53 x B57	76	B44 x B54
56	B53 x A619	77	B44 x L289
57	B53 x (B38 x B217)Selected	78	B44 x R177
58	B55 x B57	79	B52 x B54
59	B55 x A619	80	B52 x L289
60	B55 x (B38 x B217)Selected	81	B52 x R177
61	B57 x A619	82	B54 x L289
62	B57 x (B38 x B217)Selected	83	B54 x R177
63	A619 x (B38 x B217)Selected	84	L289 x R177

Table 67. Genetic effects from Model 1 and Model 2 combined over environments for date silk.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	33.89	3.60	-7.48	34.42	2.64	-7.74	0.06	-1.29	-5.65
	2	35.17	2.32	-6.33	35.36	3.20	-5.01	1.76	1.17	-5.73
	3	37.97	0.17	-7.37	38.17	2.72	-6.43	1.29	3.40	-4.86
	4	33.92	4.50	-5.89	34.66	3.62	-5.75	0.68	-1.17	-9.15
	5	34.00	4.44	-4.50	34.89	4.15	1.37	7.85	-0.39	-25.77
	6	36.39	-0.27	-7.72	35.62	2.11	-5.90	1.71	3.17	4.35
	7	31.98	-1.57	-6.13	32.34	-1.61	-6.63	-0.37	-0.06	-2.91
	8	34.38	-4.08	-7.01	34.65	-2.75	-10.54	-4.17	1.77	6.04
	9	29.08	1.23	-7.11	29.39	1.79	-8.62	-1.64	0.74	0.21
	10	29.83	1.42	-6.48	30.54	2.21	-10.77	-4.78	1.04	2.76
	11	33.79	-4.35	-8.39	33.96	-2.98	-11.16	-3.30	1.83	5.28
	12	35.23	-3.23	-7.35	35.35	-4.07	-5.71	2.11	-1.11	-6.71
	13	29.86	2.85	-7.29	29.91	-4.03	-7.86	-0.67	1.57	0.90
	14	30.90	2.08	-6.63	31.49	0.71	-11.25	-5.27	-1.83	5.02
	15	33.94	-3.38	-8.17	33.17	-4.03	-7.56	0.22	-0.86	7.49
	16	34.36	4.83	-5.86	34.66	3.05	-9.97	-4.85	-5.37	7.19
	17	34.83	4.63	-4.36	35.36	1.98	-2.90	2.16	-3.53	-10.11
	18	36.13	0.81	-9.57	35.33	4.01	-5.44	4.53	4.27	-1.33
	19	28.35	-0.11	-8.10	29.12	-0.85	-14.36	-7.18	-0.99	7.17
	20	31.57	-5.31	-9.85	31.31	-3.90	-12.39	-3.31	1.87	9.75
	21	33.08	-5.41	-7.48	33.02	-4.86	-8.96	-1.85	0.73	4.50

164

Table 67. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	29.38	-4.58	-6.09	29.64	-2.63	-6.67	-0.53	2.60	-1.57
	23	27.60	-4.52	-7.45	27.59	-5.44	-9.69	-2.77	-1.23	5.96
	24	29.13	-6.67	-7.48	28.79	-6.66	-7.82	-0.65	0.01	4.83
	25	28.30	-3.56	-5.83	28.68	-4.25	-10.51	-5.49	-0.93	7.62
	26	25.73	-3.53	-7.40	24.99	-3.36	-6.46	0.65	-0.23	6.27
	27	26.92	-2.75	-4.07	26.62	-3.84	-2.33	1.94	-1.46	-1.00
	28	32.14	1.00	-7.99	31.98	0.57	-8.30	-0.50	-0.57	2.71
	29	34.43	-1.52	-8.27	34.43	-2.67	-7.81	0.56	-1.53	-1.16
	30	33.29	1.38	-5.64	33.41	0.53	-7.45	-2.14	-1.14	3.22
	31	31.20	2.02	-8.47	31.05	2.04	-9.30	-1.12	0.03	3.87
	32	30.34	2.53	-6.95	30.07	1.42	-5.23	1.92	-1.49	-1.26
	33	34.36	-1.97	-7.14	34.49	-1.39	-7.81	-0.74	0.79	0.27
	34	31.39	0.79	-6.23	31.12	0.91	-5.85	0.27	0.16	2.23
	35	30.70	0.35	-7.66	30.53	-0.06	-9.72	-2.66	-0.54	7.32
	36	30.20	1.66	-6.82	30.33	0.94	-6.81	0.11	-0.96	-1.58
	37	34.48	3.12	-5.49	34.47	4.00	-7.58	-2.59	1.17	5.62
	38	34.01	2.97	-6.63	34.22	2.47	-7.88	-1.39	-0.67	0.74
	39	32.64	3.50	-6.14	32.80	2.00	-6.92	-0.85	-2.00	0.07
	40	30.21	0.10	-7.16	30.18	-0.24	-8.59	-1.79	-0.46	4.15
	41	29.86	0.64	-6.48	30.07	-0.61	-8.14	-1.91	-1.67	1.93
	42	29.57	1.08	-5.86	29.59	2.11	-2.06	4.70	1.37	-10.15



Table 67. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	31.61	1.35	-5.37	31.60	2.94	-5.32	0.06	2.11	-0.06
	44	28.67	1.77	-7.09	28.15	1.53	-6.95	-0.19	-0.31	5.81
	45	29.68	1.42	-5.61	29.32	0.41	-4.93	0.59	-1.34	2.44
	46	32.93	-1.51	-6.08	32.17	-0.60	-6.61	-1.18	1.21	10.32
	47	27.41	4.14	-5.57	27.07	3.19	-9.66	-5.26	-1.27	14.64
	48	34.10	-2.54	-5.54	33.59	-1.70	-3.76	1.84	1.13	1.39
	49	29.01	0.82	-6.50	28.89	-0.77	-7.93	-1.85	-2.11	5.21
	50	29.73	1.01	-6.15	29.98	0.23	-9.17	-3.54	-1.04	4.92
	51	33.47	-2.59	-5.06	33.57	-2.52	-3.69	1.75	0.10	-4.68
	52	27.56	3.40	-5.51	28.00	1.11	-9.56	-4.68	-3.06	5.31
	53	33.80	-3.62	-6.78	33.78	-4.17	-9.16	-2.94	-0.74	6.41
	54	27.58	0.03	-7.15	27.58	0.83	-10.14	-3.68	1.06	7.83
	55	31.11	-3.65	-6.65	30.83	-2.88	-8.61	-2.60	1.03	8.34
	56	25.95	2.80	-4.05	26.03	2.67	-5.04	-1.17	-0.17	1.69
	57	32.27	-4.29	-5.53	31.92	-3.34	-6.25	-1.13	1.27	5.93
	58	30.33	-3.25	-7.37	29.60	-2.59	-6.94	0.03	0.89	7.48
	59	27.20	3.10	-2.53	27.30	3.14	-5.37	-3.44	0.06	6.29
	60	32.88	-4.42	-4.40	32.45	-4.24	-2.96	1.48	0.24	1.23
	61	28.17	5.97	-6.64	27.89	3.67	-7.69	-1.49	-3.06	6.11
	62	35.70	-1.77	-6.62	35.37	-4.79	-6.13	0.38	-4.03	2.58
	63	30.01	-7.34	-5.56	30.06	-6.67	-5.74	-0.19	0.90	-0.07

Table 67. (Continued)

Type		Model 1			Model 2					
	Cross no.	m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	35.80	0.42	-6.61	35.52	-0.57	-6.15	0.36	-1.31	2.15
	65	36.98	0.46	-5.81	37.13	0.17	-8.01	-2.61	-0.39	4.03
	66	36.40	-0.05	-7.81	36.56	-0.97	-9.67	-2.19	-1.23	3.07
	67	32.81	3.07	-7.55	32.32	3.86	-7.18	0.11	1.06	4.82
	68	30.80	3.53	-9.44	30.39	2.57	-9.50	-0.36	-1.29	4.96
	69	34.05	0.67	-8.26	33.56	-1.13	-10.52	-3.12	-2.40	11.63
	70	36.73	-0.13	-5.19	37.14	-0.35	-7.05	-2.00	-0.30	0.01
	71	35.96	-0.32	-6.96	36.17	0.20	-9.00	-2.37	0.69	2.88
	72	31.93	2.68	-7.95	31.62	4.01	-6.94	1.03	1.77	1.03
	73	31.35	3.30	-6.38	30.84	2.64	-5.38	0.88	-0.89	3.42
	74	34.13	1.43	-7.87	34.20	2.96	-8.68	-0.96	2.04	1.34
	75	36.52	-0.02	-7.04	36.87	0.05	-9.32	-2.58	0.09	1.91
	76	32.52	2.77	-9.09	32.73	4.33	-11.42	-2.73	2.09	3.62
	77	31.40	3.49	-9.49	31.76	3.74	-12.14	-3.02	0.33	2.74
	78	35.89	0.82	-6.81	36.68	0.41	-10.31	-3.77	-0.54	-0.17
	79	32.70	2.77	-6.90	32.16	3.99	-5.10	1.84	1.63	1.72
	80	32.77	4.28	-6.96	33.10	5.35	-8.33	-1.46	1.43	-0.29
	81	34.52	0.99	-7.53	34.46	0.72	-6.87	0.77	-0.36	-1.00
	82	29.87	0.83	-6.94	29.89	0.04	-8.43	-1.82	-1.06	3.74
	83	30.77	-1.67	-9.95	30.85	-2.11	-11.63	-2.01	-0.59	3.37
	84	31.07	-2.76	-7.77	31.29	-3.26	-9.17	-1.57	-0.67	1.03

Table 68. Genetic effects from Model 1 and Model 2 combined over environments for plant height.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	191.61	14.37	50.88	192.92	14.48	63.50	16.45	0.15	-48.33
	2	202.83	6.83	64.71	201.92	1.71	74.23	11.09	-6.82	-14.03
	3	222.15	-16.89	60.00	220.78	-24.09	65.80	6.19	-9.59	1.11
	4	206.53	1.23	55.41	207.09	0.45	58.09	3.70	-1.04	-13.69
	5	187.67	12.91	51.38	187.23	4.58	72.31	25.47	-11.10	-49.36
	6	199.31	9.74	60.26	199.26	7.22	64.70	5.44	-3.37	-11.01
	7	194.07	-6.97	67.47	195.36	-10.15	59.17	-9.33	-4.25	6.40
	8	206.22	-27.64	57.47	205.50	-27.13	71.41	16.67	0.67	-27.87
	9	191.28	-12.71	48.38	191.88	-10.30	40.84	-8.87	3.22	12.56
	10	178.06	1.99	49.03	180.87	0.88	46.70	-0.92	-1.49	-27.19
	11	189.21	-5.01	55.91	193.00	-8.86	46.56	-8.88	-5.14	-20.48
	12	216.23	-20.20	63.54	215.90	-12.09	82.09	22.62	10.81	-44.49
	13	203.38	-1.89	58.45	205.94	11.75	46.24	-13.26	18.18	1.49
	14	195.40	8.34	68.71	198.77	10.18	57.54	-11.41	2.45	-10.72
	15	208.81	2.29	79.99	213.45	3.02	68.13	-11.40	0.97	-23.83
	16	214.40	16.96	47.57	213.58	19.07	54.80	8.33	2.81	-9.13
	17	211.70	25.59	64.88	212.69	15.59	65.92	1.97	-13.33	-14.44
	18	217.93	21.60	66.46	218.82	14.06	64.98	-1.21	-10.05	-6.67
	19	187.58	10.84	47.52	189.00	1.71	53.43	8.27	-12.17	-32.22
	20	199.14	8.24	57.50	200.32	7.08	49.95	-8.48	-1.55	5.77
	21	185.09	-7.16	56.15	187.78	-11.40	53.95	-0.84	-5.66	-26.06

Table 68. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	178.18	-15.32	61.03	182.68	-14.68	57.16	-1.65	0.85	-43.06
	23	173.49	-16.45	55.77	177.40	-20.93	54.91	1.66	-5.98	-44.02
	24	171.71	-18.57	44.74	174.85	-23.56	35.16	-9.61	-6.66	-12.19
	25	167.93	-10.79	56.53	168.58	-9.29	49.89	-7.73	2.01	9.64
	26	178.50	-17.65	58.12	184.22	-24.92	37.21	-21.78	-9.70	-12.97
	27	163.91	-20.16	39.62	163.51	-18.53	49.72	12.16	2.17	-21.63
	28	189.98	0.52	58.79	192.64	0.10	50.34	-8.55	-0.57	-9.44
	29	188.94	-0.30	54.81	190.76	2.19	55.51	2.12	3.31	-23.25
	30	183.96	3.20	62.39	183.92	1.30	71.22	10.85	-2.54	-22.61
	31	199.52	0.61	71.67	204.93	-4.82	62.40	-7.66	-7.24	-39.74
	32	187.13	-3.66	56.56	185.48	-2.30	66.75	11.41	1.81	-7.15
	33	188.33	-2.36	58.34	188.89	-2.86	60.39	2.92	-0.67	-11.96
	34	182.40	1.64	57.72	183.13	-0.12	68.53	13.83	-2.35	-36.75
	35	196.75	-2.66	69.34	201.23	-13.55	50.93	-19.56	-14.53	-4.96
	36	184.79	-4.73	46.68	185.22	-4.39	56.15	11.96	0.45	-29.72
	37	187.26	4.47	58.91	189.12	1.05	59.56	2.10	-4.57	-23.72
	38	196.89	1.37	68.00	200.77	-3.84	65.26	-0.68	-6.95	-38.68
	39	192.96	-2.07	56.92	193.42	0.31	58.08	1.75	3.17	-8.47
	40	192.47	-3.60	74.12	195.03	-5.92	73.30	0.77	-3.10	-28.09
	41	183.38	-8.10	54.28	182.19	-10.33	65.24	12.67	-2.98	-14.50
	42	194.86	-5.13	63.48	197.76	-4.45	72.49	13.11	0.91	-57.70

Table 68. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	177.48	-1.39	56.37	178.17	4.76	62.66	8.24	8.20	-24.65
	44	172.49	-7.42	38.08	171.84	-4.37	41.75	4.07	4.07	-1.87
	45	181.23	-8.27	53.36	180.28	-1.53	59.32	6.67	8.99	-4.27
	46	177.26	-3.00	53.86	178.32	-0.46	56.90	4.49	3.38	-20.44
	47	165.02	8.63	53.10	166.70	8.86	47.66	-5.54	0.30	-5.61
	48	179.85	-8.95	49.33	180.95	-10.86	51.87	3.90	-2.54	-19.62
	49	181.42	-6.31	51.66	179.89	-9.59	59.05	8.03	-4.38	-1.15
	50	183.32	-4.19	50.54	182.94	4.23	67.29	20.37	11.22	-39.24
	51	184.37	-0.78	64.53	183.99	-1.90	69.58	5.96	-1.50	-8.67
	52	167.61	11.75	52.51	168.52	7.34	45.16	-8.43	-5.89	8.44
	53	186.57	-4.62	57.27	186.70	-7.58	57.39	0.24	-3.94	-1.81
	54	181.18	-0.19	39.90	178.87	4.45	49.25	9.91	6.18	2.97
	55	185.50	6.54	57.53	184.55	10.58	53.87	-5.17	5.39	20.78
	56	169.58	17.66	44.38	171.23	18.33	39.32	-5.09	0.89	-6.27
	57	187.82	0.54	53.09	186.53	2.27	53.50	-0.40	2.31	14.22
	58	182.10	7.21	44.54	182.22	8.09	45.50	1.26	1.17	-3.91
	59	165.42	18.26	38.09	165.77	11.52	38.98	1.33	-8.98	-6.39
	60	189.84	1.88	56.18	188.21	1.92	63.54	7.94	0.06	0.09
	61	166.45	11.72	48.71	167.39	9.16	42.74	-6.70	-3.42	4.41
	62	182.21	-4.74	59.68	179.23	-7.14	73.38	14.80	-3.21	-0.44
	63	172.60	-19.76	51.76	173.98	-26.21	47.72	-4.02	-8.60	-5.80

Table 68. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	185.69	19.90	65.46	185.32	23.98	75.36	11.95	5.43	-21.54
	65	185.57	21.64	65.71	187.82	21.49	63.00	-1.79	-0.20	-19.48
	66	207.46	0.28	70.71	206.54	5.69	80.48	11.40	7.21	-14.66
	67	205.85	10.19	76.20	208.30	10.66	69.06	-7.08	0.62	-10.40
	68	203.92	0.71	61.67	202.98	7.95	72.57	12.77	9.65	-17.26
	69	209.04	11.33	78.11	211.38	26.75	88.77	14.76	20.55	-55.54
	70	159.49	4.18	53.48	160.39	6.37	58.73	7.09	2.92	-24.29
	71	187.80	-19.17	64.92	187.43	-17.11	69.65	5.58	2.75	-8.05
	72	186.78	-10.43	70.70	191.11	-14.18	60.96	-9.00	-5.00	-25.74
	73	187.02	-17.79	57.92	188.45	-9.02	61.09	4.90	11.69	-25.19
	74	187.53	-14.55	71.19	190.88	-22.14	66.67	-3.25	-10.13	-27.73
	75	184.03	-22.69	63.04	185.03	-19.88	67.56	6.26	3.75	-23.65
	76	179.70	-12.94	67.51	182.92	-11.46	62.04	-4.51	1.97	-23.76
	77	186.20	-20.77	58.22	190.19	-7.74	63.35	9.10	17.38	-60.50
	78	186.02	-16.56	71.43	189.88	-20.08	54.82	-17.78	-4.70	-2.22
	79	204.69	10.33	70.53	207.65	12.03	67.86	-1.24	2.26	-28.06
	80	205.70	-0.96	55.72	206.86	-0.58	52.55	-3.10	0.51	-5.37
	81	206.20	5.66	64.18	210.64	-2.64	56.28	-6.64	-11.07	-31.98
	82	204.89	-7.93	72.43	207.59	1.69	73.39	3.06	12.03	-34.49
	83	200.17	-4.37	68.61	206.71	-10.37	57.16	-9.56	-8.00	-47.46
	84	199.07	5.88	51.49	203.10	-4.09	46.10	-3.84	-13.30	-33.60

Table 69. Genetic effects from Model 1 and Model 2 combined over environments for ear height.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	93.10	20.72	24.78	93.89	21.72	30.37	7.43	1.34	-23.90
	2	109.35	9.27	39.98	108.39	7.42	52.55	14.81	-2.46	-21.45
	3	124.97	-9.46	36.92	123.68	-13.44	44.27	8.17	-5.31	-3.96
	4	109.30	8.51	33.10	109.88	10.12	40.86	9.96	2.14	-27.07
	5	95.21	14.80	27.97	94.72	10.25	50.58	27.52	-6.07	-53.22
	6	109.21	7.01	33.92	109.08	4.88	37.37	4.15	-2.83	-7.39
	7	89.48	-10.38	34.84	89.77	-9.04	32.15	-3.11	1.79	3.61
	8	101.12	-27.66	31.57	99.45	-26.95	38.23	7.04	0.94	2.37
	9	84.60	-12.32	24.53	83.58	-11.31	21.57	-4.36	1.34	19.77
	10	76.81	-3.47	23.04	77.99	-4.75	23.60	1.51	-1.70	-15.39
	11	90.22	-13.01	29.04	92.34	-14.35	24.32	-4.33	-1.78	-12.81
	12	116.74	-16.76	37.84	116.60	-14.74	52.05	17.40	2.70	-35.38
	13	99.50	1.05	32.45	99.79	9.43	32.91	0.77	11.17	-4.65
	14	98.46	7.90	43.34	99.84	8.88	36.30	-7.71	1.31	2.04
	15	107.37	-2.65	39.97	109.62	-6.26	30.33	-10.31	-4.82	-1.47
	16	111.14	16.38	23.35	110.97	14.77	28.43	6.15	-2.15	-11.31
	17	113.16	22.02	39.94	114.51	15.83	44.52	6.59	-8.25	-27.90
	18	117.15	13.94	31.59	117.53	9.68	30.07	-1.61	-5.69	-0.54
	19	89.76	7.55	25.43	91.11	4.43	33.22	10.53	-4.16	-36.36
	20	101.24	-0.97	28.89	102.20	-3.76	28.05	-0.37	-3.72	-9.17
	21	91.26	-10.75	27.82	92.53	-16.07	27.30	0.24	-7.09	-13.66

Table 69. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	64.10	-16.03	29.33	65.62	-14.27	27.38	-1.34	2.35	-12.94
	23	62.76	-18.06	25.04	64.59	-20.79	29.68	6.99	-3.64	-33.80
	24	61.03	-14.85	23.67	63.08	-18.38	17.94	-5.63	-4.71	-9.30
	25	64.11	-15.13	33.31	64.20	-16.46	26.65	-8.14	-1.77	16.28
	26	60.09	-14.32	23.94	63.18	-20.00	13.50	-10.71	-7.58	-9.38
	27	57.93	-18.37	19.27	57.25	-18.30	21.08	1.76	0.09	3.23
	28	80.92	-0.61	33.88	80.61	0.29	30.55	-4.32	1.20	12.33
	29	81.72	2.00	33.48	83.92	0.96	31.33	-1.13	-1.39	-20.43
	30	81.22	0.26	38.39	81.21	-2.59	47.20	10.84	-3.80	-22.87
	31	85.54	2.60	43.26	88.90	-3.51	38.11	-4.00	-8.14	-26.33
	32	78.96	-0.82	29.47	77.88	2.92	33.24	3.89	4.99	2.93
	33	80.66	2.55	34.59	81.20	1.36	37.55	4.02	-1.58	-14.12
	34	82.69	0.26	38.08	82.71	-3.86	43.64	6.86	-5.50	-14.68
	35	83.99	3.72	40.72	86.22	-1.89	32.91	-8.07	-7.48	-5.94
	36	77.09	-1.04	22.10	77.01	-0.28	33.12	13.51	1.01	-27.84
	37	86.25	-2.34	44.24	88.25	-5.07	33.53	-11.80	-3.64	4.28
	38	84.24	0.30	40.12	89.03	-5.52	31.46	-7.33	-7.76	-34.15
	39	83.29	-1.62	35.00	84.41	6.79	28.68	-7.01	11.22	3.31
	40	84.23	2.04	45.30	86.59	-0.37	40.56	-4.20	-3.21	-15.57
	41	83.49	-2.58	37.61	83.26	-2.18	40.07	2.88	0.53	-3.77
	42	81.05	-6.22	33.04	83.45	-6.20	37.62	7.32	0.03	-40.41



Table 69. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	75.02	-2.18	32.19	75.37	1.73	37.87	7.24	5.21	-18.98
	44	69.84	-6.17	20.00	67.92	-6.09	24.80	4.58	0.10	10.22
	45	73.92	-5.90	27.71	72.35	-4.72	29.03	0.54	1.58	15.10
	46	76.49	-7.27	25.02	75.75	-1.38	29.34	4.82	7.86	-2.59
	47	56.01	10.47	23.23	55.92	7.60	19.72	-4.39	-3.83	10.24
	48	71.43	-3.82	28.26	71.14	-7.84	31.87	4.23	-5.36	-5.92
	49	84.61	-3.25	39.96	83.92	-3.24	42.20	2.28	0.01	2.25
	50	83.64	-1.34	33.60	84.27	3.94	31.17	-2.54	7.04	-1.21
	51	88.21	-4.00	43.33	87.43	1.31	53.19	11.60	7.08	-16.47
	52	65.75	16.03	32.85	66.88	16.65	25.37	-8.42	0.83	6.09
	53	85.65	1.61	43.70	87.14	-0.03	39.09	-4.63	-2.19	-5.67
	54	74.66	0.91	18.97	72.43	3.74	25.48	6.47	3.78	9.40
	55	84.12	-1.47	31.31	81.83	3.41	30.05	-3.14	6.51	30.36
	56	60.21	19.15	18.39	60.64	21.79	14.78	-4.14	3.52	4.29
	57	82.41	4.51	36.43	82.10	6.80	32.95	-4.51	3.06	12.79
	58	77.70	-3.02	16.68	76.24	-3.44	22.85	6.59	-0.56	1.17
	59	58.03	18.63	15.96	58.69	19.16	19.06	4.27	0.70	-15.86
	60	79.39	2.84	31.97	79.01	-0.21	36.51	5.34	-4.07	-7.42
	61	60.80	20.23	18.91	59.39	16.75	23.24	4.36	-4.63	5.32
	62	83.49	5.47	37.67	81.99	-1.37	46.31	9.60	-9.12	-4.82
	63	61.87	-16.45	28.23	62.97	-23.85	22.15	-6.73	-9.87	2.84

Table 69. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	80.86	10.00	34.74	79.65	14.65	46.79	14.01	6.20	-17.21
	65	80.96	12.32	39.58	81.03	12.01	47.71	10.05	-0.42	-21.98
	66	99.51	-2.20	44.39	98.73	1.60	47.98	3.87	5.06	-0.10
	67	89.98	10.34	44.51	91.46	11.13	43.13	-0.68	1.05	-13.83
	68	93.77	-3.04	31.98	93.09	-0.18	39.29	8.53	3.81	-11.07
	69	85.17	18.83	40.97	88.82	31.32	43.52	5.68	16.65	-49.83
	70	67.79	5.13	29.58	67.79	8.65	33.90	5.32	4.69	-11.21
	71	90.06	-13.10	40.33	89.92	-14.99	40.10	-0.37	-2.51	2.25
	72	81.09	-0.42	41.56	83.65	-3.93	35.36	-5.87	-4.67	-14.04
	73	84.85	-12.52	27.00	85.86	-10.68	29.24	3.47	2.46	-17.89
	74	71.49	5.25	33.87	74.18	2.01	26.85	-6.78	-4.32	-13.52
	75	85.75	-16.35	37.40	86.89	-17.95	39.44	3.31	-2.13	-18.86
	76	72.68	-4.96	34.87	74.71	-9.67	35.58	2.29	-6.28	-25.84
	77	87.93	-16.26	35.29	90.83	-12.90	35.55	2.35	4.48	-35.09
	78	72.24	2.38	40.90	75.53	-0.54	32.76	-7.74	-3.89	-17.70
	79	94.22	13.71	43.43	96.70	17.01	41.55	-0.59	4.40	-24.45
	80	102.16	-0.47	33.08	103.83	0.63	30.51	-2.01	1.46	-13.02
	81	85.82	17.13	36.50	88.78	12.88	25.66	-11.30	-5.67	-6.79
	82	92.90	-12.91	42.82	94.61	-7.57	42.81	1.18	7.12	-20.18
	83	77.06	5.11	41.62	81.00	4.62	25.06	-17.65	-0.65	-3.44
	84	78.18	18.22	21.01	81.22	13.80	18.12	-1.45	-5.89	-28.46

Table 70. Genetic effects from Model 1 and Model 2 combined over environments for kernel row number.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	16.31	-0.61	2.78	16.42	-0.85	2.22	-0.62	-0.33	0.22
	2	15.93	-0.32	2.56	15.92	-0.38	3.19	0.76	-0.07	-1.52
	3	14.69	0.68	1.82	14.71	0.80	2.07	0.32	0.15	-0.91
	4	13.36	1.65	0.94	13.50	1.67	0.62	-0.30	0.02	-0.78
	5	16.12	-0.83	1.28	16.18	-0.25	0.92	-0.41	0.78	0.31
	6	15.35	0.37	1.81	15.72	0.33	1.10	-0.62	-0.05	-2.48
	7	16.74	0.24	2.91	16.85	0.63	2.96	0.13	0.52	-1.36
	8	16.33	0.94	3.55	16.55	0.62	3.83	0.49	-0.42	-3.32
	9	13.72	2.08	1.24	13.66	2.22	1.63	0.44	0.19	-0.26
	10	17.21	-0.66	2.36	17.32	-0.53	2.63	0.41	0.17	-2.07
	11	16.18	0.66	2.73	16.44	0.24	2.32	-0.32	-0.55	-2.05
	12	15.23	0.82	1.68	15.38	0.65	1.31	-0.36	-0.23	-0.71
	13	13.73	1.95	1.08	13.81	1.77	0.54	-0.62	-0.25	0.58
	14	16.36	-0.73	1.03	16.42	-0.80	1.71	0.88	-0.09	-2.41
	15	15.74	0.80	1.92	15.99	1.02	1.30	-0.60	0.30	-1.29
	16	12.34	0.87	0.19	12.38	0.53	0.03	-0.18	-0.45	-0.05
	17	15.53	-1.53	1.52	15.49	-1.41	1.72	0.22	0.16	-0.03
	18	14.57	-0.47	1.64	14.75	-1.25	0.09	-1.78	-1.03	1.82
	19	13.79	-2.72	0.20	13.67	-2.86	0.52	0.32	-0.18	0.59
	20	13.32	-1.30	1.34	13.54	-1.69	0.98	-0.29	-0.53	-1.74
	21	15.75	1.31	1.35	15.77	0.90	1.59	0.30	-0.54	-0.79

Table 70. (Continued)

Type		Model 1			Model 2					
Cross no.		m	a	d	m	a	d	aa	ad	dd
Type II										
22		14.86	0.42	0.87	14.97	0.82	1.01	0.26	0.53	-1.72
23		15.41	0.18	1.29	15.58	0.24	0.99	-0.26	0.09	-1.19
24		15.73	0.24	2.32	15.90	-0.17	1.86	-0.45	-0.55	-0.80
25		15.44	0.08	1.25	15.59	-0.10	0.81	-0.44	-0.11	-0.65
26		14.97	0.30	1.32	15.19	-0.64	0.99	-0.25	-1.26	-1.82
27		16.29	-0.99	1.45	16.31	-1.16	1.01	-0.53	-0.23	0.88
28		14.68	-0.18	0.43	14.91	-0.43	0.40	0.12	-0.33	-2.58
29		14.97	-0.10	1.46	15.11	-0.96	1.02	-0.45	-1.14	-0.54
30		14.66	-0.33	0.59	14.73	-0.73	-0.06	-0.75	-0.54	0.81
31		14.97	-0.04	1.59	15.21	-1.08	0.90	-0.70	-1.38	-0.94
32		15.51	-1.22	0.42	15.50	-1.44	-0.49	-1.12	-0.29	2.46
33		15.27	0.07	2.13	15.30	-0.53	2.31	0.24	-0.79	-0.89
34		14.92	-0.16	0.53	15.10	-0.51	0.40	-0.04	-0.46	-1.72
35		15.33	0.26	1.84	15.69	-0.53	1.09	-0.68	-1.05	-2.24
36		16.00	-1.04	1.01	16.09	-1.38	1.11	0.18	-0.45	-1.26
37		15.40	-0.11	1.81	15.62	0.30	0.99	-0.86	0.54	-0.40
38		15.49	0.26	2.42	15.93	0.37	1.11	-1.31	0.14	-1.76
39		16.33	-1.03	2.05	16.47	-0.35	2.07	0.13	0.90	-1.70
40		14.85	0.33	1.23	15.12	-0.32	1.09	0.01	-0.87	-2.82
41		15.97	-0.88	0.71	16.07	-0.44	0.37	-0.34	0.59	-0.38
42		15.64	-1.33	1.31	15.67	-0.54	1.69	0.50	1.06	-1.43

Table 70. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	15.80	0.11	2.23	15.94	0.57	1.84	-0.38	0.61	-0.59
	44	16.07	-0.44	2.11	16.09	-0.28	1.97	-0.16	0.21	0.18
	45	16.06	-0.68	1.54	16.09	-0.18	2.02	0.61	0.66	-1.61
	46	15.25	0.15	1.24	15.49	0.33	1.13	0.04	0.25	-2.56
	47	15.35	0.13	1.31	15.52	0.68	1.20	-0.01	0.73	-1.66
	48	15.44	0.22	2.00	15.67	-0.03	2.12	0.31	-0.33	-3.09
	49	15.61	-0.55	1.21	15.60	-0.79	0.90	-0.38	-0.32	0.88
	50	15.96	-0.57	0.57	16.15	0.23	0.03	-0.54	1.06	-0.77
	51	15.24	0.19	1.61	15.28	0.02	1.18	-0.50	-0.22	0.67
	52	15.51	0.02	1.48	15.65	0.28	1.09	-0.39	0.34	-0.67
	53	15.52	0.22	2.39	15.64	-0.22	2.70	0.46	-0.58	-2.26
	54	16.51	-0.37	1.47	16.50	-0.50	1.93	0.55	-0.17	-1.06
	55	15.69	0.39	1.93	15.61	0.12	2.15	0.22	-0.37	0.35
	56	16.13	0.48	2.27	16.15	0.75	2.02	-0.30	0.35	0.40
	57	15.87	0.74	2.32	15.88	0.82	2.73	0.51	0.11	-1.26
	58	15.61	0.87	0.98	15.59	0.63	1.32	0.41	-0.32	-0.67
	59	16.36	0.73	1.90	16.42	0.80	1.74	-0.15	0.10	-0.32
	60	16.04	0.97	1.57	16.31	0.57	2.27	1.06	-0.53	-5.13
	61	15.20	-0.06	1.45	15.25	0.20	1.51	0.11	0.34	-0.72
	62	15.13	-0.01	1.64	15.31	-0.71	0.75	-0.98	-0.94	0.24
	63	15.95	0.11	2.73	16.19	-0.53	2.33	-0.32	-0.85	-1.87

Table 70. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	15.85	-1.40	3.76	16.10	-2.69	4.73	1.37	-1.71	-5.44
	65	14.56	-0.52	1.94	14.64	-0.46	2.08	0.22	0.09	-1.24
	66	15.36	-1.30	2.15	15.49	-1.05	2.17	0.11	0.33	-1.54
	67	14.77	-0.38	1.95	15.24	-0.58	0.29	-1.71	-0.27	-1.29
	68	12.90	0.89	1.54	13.00	1.25	1.49	0.01	0.49	-1.06
	69	14.39	0.74	2.96	15.03	0.59	2.24	-0.44	-0.20	-5.72
	70	16.45	0.62	3.27	16.76	1.38	2.85	-0.31	1.02	-2.53
	71	17.39	0.17	3.55	17.74	1.98	3.39	0.05	2.42	-3.77
	72	16.66	1.24	3.19	17.35	2.80	2.18	-0.77	2.08	-5.50
	73	14.77	2.43	2.76	15.02	4.38	1.97	-0.81	2.59	-0.83
	74	15.83	1.99	3.94	16.46	2.87	2.68	-1.11	1.17	-4.25
	75	16.40	-0.81	2.98	16.50	-0.72	2.97	0.06	0.11	-1.18
	76	15.86	0.23	3.28	16.18	0.05	1.65	-1.78	-0.24	0.42
	77	14.04	1.73	1.76	14.43	2.53	1.16	-0.47	1.07	-3.04
	78	14.70	1.25	2.55	15.18	0.58	0.90	-1.69	-0.90	-1.39
	79	15.47	1.03	1.29	15.71	0.70	1.00	-0.19	-0.45	-2.17
	80	14.06	2.05	1.30	14.06	1.68	0.13	-1.44	-0.49	3.03
	81	14.70	1.66	2.07	14.92	0.44	1.49	-0.57	-1.62	-1.03
	82	13.01	1.31	0.76	13.23	1.80	-0.36	-1.23	0.65	0.25
	83	13.97	0.95	1.91	14.47	0.64	0.59	-1.27	-0.41	-2.50
	84	12.40	-0.25	1.64	12.66	-0.77	0.80	-0.86	-0.69	-0.87

Table 71. Genetic effects from Model 1 and Model 2 combined over environments for ear length.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	15.72	1.29	4.74	16.07	2.34	4.59	0.06	1.40	-3.75
	2	15.60	1.73	5.71	15.97	1.62	5.36	-0.17	-0.14	-3.52
	3	18.14	-1.10	6.45	18.15	-1.20	7.53	1.33	-0.14	-2.85
	4	18.15	-0.39	7.30	18.19	0.07	6.68	-0.74	0.62	1.17
	5	16.41	2.06	7.45	16.75	2.21	8.32	1.30	0.20	-6.22
	6	15.79	1.90	5.73	16.24	2.81	5.22	-0.32	1.22	-3.93
	7	14.08	0.40	4.78	14.35	-0.44	3.16	-1.81	-1.13	0.95
	8	16.30	-2.80	4.34	16.48	-5.21	5.03	0.97	-3.21	-3.85
	9	16.13	-1.62	5.91	15.87	-1.72	6.18	0.15	-0.13	2.36
	10	13.77	0.85	4.78	13.89	0.88	4.56	-0.18	0.03	-0.88
	11	14.11	0.36	4.58	14.42	-0.31	3.61	-0.98	-0.89	-1.13
	12	16.40	-2.83	5.28	16.91	-2.46	5.79	0.98	0.49	-7.30
	13	16.30	-2.20	6.82	16.39	-1.92	5.69	-1.34	0.38	1.90
	14	14.28	0.16	6.77	14.61	0.81	5.24	-1.65	0.87	0.06
	15	14.77	0.06	7.50	15.10	1.25	6.98	-0.40	1.59	-2.61
	16	18.26	0.41	5.60	18.22	0.25	5.45	-0.21	-0.21	0.91
	17	16.44	3.07	5.82	16.66	3.63	5.75	0.06	0.74	-2.37
	18	16.56	2.81	5.20	16.86	2.71	4.14	-1.10	-0.13	-0.74
	19	15.65	2.16	6.45	15.50	1.76	7.02	0.59	-0.54	0.30
	20	15.70	2.12	5.73	15.72	2.27	5.91	0.24	0.21	-0.67
	21	12.90	-0.11	4.18	13.11	0.31	3.10	-1.19	0.55	0.42

Table 71. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	16.51	-1.78	4.10	16.52	-1.71	2.53	-1.93	0.10	4.03
	23	14.66	-0.90	2.72	14.71	-0.96	3.86	1.43	-0.08	-3.57
	24	15.08	-1.69	1.67	15.39	-2.76	2.08	0.72	-1.43	-4.71
	25	15.93	-1.32	4.06	16.02	-1.57	3.72	-0.36	-0.33	-0.16
	26	15.11	-0.35	4.73	15.46	-1.71	3.94	-0.74	-1.81	-2.06
	27	15.16	-2.51	0.82	15.01	-1.97	2.68	2.19	0.72	-3.11
	28	16.95	0.75	3.76	17.00	0.35	4.50	0.94	-0.53	-2.47
	29	17.22	0.62	3.58	17.15	1.13	4.26	0.78	0.67	-0.90
	30	17.65	0.85	4.55	17.60	2.00	5.59	1.25	1.53	-2.14
	31	16.81	1.86	5.46	16.88	1.65	6.73	1.62	-0.28	-4.20
	32	17.79	-0.84	3.21	17.42	-1.02	5.66	2.76	-0.25	-1.99
	33	16.22	-0.62	3.33	16.27	-0.93	5.04	2.15	-0.41	-5.11
	34	16.78	-0.68	3.80	17.00	-0.96	3.38	-0.36	-0.38	-1.53
	35	15.58	0.75	4.59	15.73	-0.61	4.07	-0.54	-1.81	-0.44
	36	16.37	-1.56	1.97	16.14	-1.19	4.05	2.40	0.49	-2.67
	37	16.63	0.27	3.41	16.52	0.76	5.17	2.10	0.66	-3.33
	38	16.49	1.03	5.58	16.50	-0.41	5.78	0.26	-1.92	-0.67
	39	17.31	-1.14	3.13	16.91	-0.62	4.98	2.01	0.70	-0.12
	40	16.84	1.31	6.34	16.93	0.66	7.39	1.36	-0.87	-3.89
	41	17.74	-1.34	2.96	17.70	-1.78	4.68	2.08	-0.58	-3.96
	42	16.93	-2.45	4.31	16.91	-1.41	6.14	2.24	1.38	-4.46



Table 71. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	17.24	0.02	4.51	17.30	0.52	5.58	1.36	0.67	-3.46
	44	15.81	0.65	3.33	15.66	0.79	3.46	0.05	0.18	1.48
	45	18.01	-1.32	3.89	17.76	-0.68	4.72	0.91	0.85	-0.34
	46	16.53	0.96	5.03	16.49	1.21	5.09	0.05	0.33	0.32
	47	16.61	1.75	5.51	16.89	2.66	6.04	0.85	1.21	-4.62
	48	17.23	-0.26	4.29	17.25	-0.25	4.37	0.10	0.01	-0.39
	49	15.99	0.57	3.93	15.82	0.10	6.60	3.16	-0.62	-4.89
	50	18.05	-1.19	4.00	17.82	-0.40	7.17	3.75	1.05	-5.58
	51	16.23	0.70	4.25	16.16	0.28	4.66	0.46	-0.57	-0.27
	52	15.84	1.43	3.84	16.04	1.14	3.37	-0.45	-0.38	-1.14
	53	16.49	-0.19	3.07	16.44	-0.44	5.22	2.61	-0.33	-4.94
	54	16.24	-1.83	2.46	15.76	-1.12	5.79	3.77	0.95	-3.06
	55	15.36	0.10	4.31	15.18	-0.12	5.25	1.04	-0.30	-0.38
	56	14.99	0.70	3.35	15.20	0.12	3.19	-0.05	-0.78	-2.07
	57	16.14	-1.02	3.76	15.95	-1.26	4.99	1.39	-0.33	-1.03
	58	17.51	2.10	3.95	17.44	1.48	4.82	1.02	-0.82	-1.39
	59	15.21	2.81	0.85	15.09	2.17	2.70	2.20	-0.86	-3.37
	60	17.25	1.11	3.03	16.60	0.82	4.77	1.68	-0.39	3.12
	61	15.15	0.62	4.29	15.33	1.03	4.02	-0.20	0.55	-1.45
	62	16.07	-1.07	4.38	15.79	-1.37	5.52	1.21	-0.40	0.30
	63	15.13	-1.75	2.49	15.19	-2.29	2.92	0.57	-0.72	-1.84

Table 71. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV	64	14.88	-1.25	7.02	15.19	-0.34	5.50	-1.66	1.21	0.28
	65	15.40	-1.65	6.58	15.86	-1.37	3.99	-2.87	0.37	1.31
	66	16.39	-2.98	7.50	16.68	-3.26	7.85	0.63	-0.37	-4.32
	67	15.35	-1.57	7.71	15.73	-1.86	6.33	-1.44	-0.38	-0.82
	68	16.25	-2.63	7.83	16.03	-2.13	5.83	-2.61	0.66	7.73
	69	16.50	0.07	8.98	17.71	2.61	8.49	0.24	3.39	-13.05
	70	14.97	-0.56	4.19	15.02	-0.72	4.91	0.92	-0.22	-2.43
	71	16.32	-1.40	5.34	16.24	-1.41	7.17	2.19	-0.01	-3.71
	72	16.04	0.26	6.39	16.34	0.48	6.93	0.87	0.30	-4.96
	73	16.58	-1.51	5.38	16.65	-1.83	5.46	0.15	-0.43	-1.04
	74	15.65	0.18	6.71	16.02	-1.19	6.58	0.09	-1.82	-4.01
	75	16.93	-0.93	5.78	16.81	-0.87	7.63	2.19	0.08	-3.35
	76	15.97	0.51	5.53	16.22	1.15	4.73	-0.80	0.85	-0.92
	77	16.63	-0.86	4.71	16.76	-0.72	6.14	1.86	0.19	-5.29
	78	16.34	0.84	6.71	16.86	-0.24	6.20	-0.28	-1.44	-4.77
	79	17.15	1.47	6.44	17.25	1.77	7.81	1.75	0.40	-4.71
	80	18.42	-0.00	6.33	18.41	-0.12	6.64	0.37	-0.15	-0.74
	81	17.72	1.94	7.76	18.18	1.37	6.50	-1.23	-0.76	-2.21
	82	17.25	-1.13	6.03	17.56	-0.70	5.31	-0.67	0.58	-1.81
	83	15.73	0.25	6.70	16.10	-1.30	5.61	-1.08	-2.06	-1.54
	84	17.81	1.79	8.64	18.07	1.22	7.24	-1.55	-0.76	0.60

Table 72. Genetic effects from Model 1 and Model 2 combined over environments for ear diameter.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	4.37	-0.19	0.80	4.40	-0.15	0.80	0.02	0.06	-0.30
	2	4.38	-0.16	0.93	4.40	-0.28	0.80	-0.14	-0.17	0.03
	3	4.05	0.11	0.78	4.08	0.08	0.75	-0.01	-0.05	-0.38
	4	3.92	0.15	0.45	3.97	0.18	0.33	-0.12	0.04	-0.30
	5	4.31	-0.17	0.68	4.32	-0.15	0.85	0.22	0.03	-0.62
	6	4.31	0.02	0.99	4.37	0.05	0.84	-0.14	0.05	-0.36
	7	4.46	0.04	0.75	4.48	-0.08	0.64	-0.12	-0.16	0.05
	8	4.35	0.28	0.89	4.42	0.10	1.04	0.23	-0.24	-1.22
	9	4.18	0.27	0.64	4.22	0.17	0.53	-0.11	-0.13	-0.17
	10	4.52	-0.01	0.66	4.55	0.03	0.75	0.13	0.05	-0.61
	11	4.50	0.13	0.99	4.55	-0.06	0.92	-0.05	-0.26	-0.43
	12	4.29	0.24	0.94	4.36	0.27	0.77	-0.15	0.03	-0.43
	13	4.14	0.27	0.74	4.18	0.32	0.66	-0.06	0.06	-0.27
	14	4.45	-0.04	0.60	4.50	0.10	0.68	0.14	0.19	-0.87
	15	4.50	0.13	1.01	4.59	0.17	0.78	-0.22	0.06	-0.48
	16	3.83	-0.05	0.55	3.87	-0.12	0.37	-0.19	-0.09	-0.01
	17	4.20	-0.30	0.70	4.23	-0.22	0.81	0.16	0.10	-0.64
	18	4.20	-0.18	0.95	4.27	-0.34	0.61	-0.37	-0.22	0.00
	19	4.07	-0.36	0.47	4.09	-0.43	0.56	0.12	-0.09	-0.43
	20	4.18	-0.14	0.89	4.27	-0.25	0.66	-0.21	-0.15	-0.47
	21	4.36	0.16	0.76	4.38	0.06	0.74	-0.00	-0.14	-0.22

Table 72. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	4.47	0.21	0.56	4.49	0.21	0.83	0.35	-0.01	-0.91
	23	4.62	0.13	0.74	4.66	-0.16	0.75	0.05	-0.39	-0.60
	24	4.56	0.24	0.73	4.60	0.11	0.56	-0.18	-0.18	0.30
	25	4.44	0.27	0.56	4.43	0.28	0.69	0.16	0.02	-0.28
	26	4.51	0.28	0.75	4.57	0.05	0.53	-0.23	-0.31	-0.13
	27	4.47	0.09	0.31	4.45	0.16	0.32	-0.00	0.09	0.21
	28	4.39	-0.01	0.75	4.44	-0.08	0.84	0.15	-0.09	-0.86
	29	4.34	0.03	0.71	4.39	-0.07	0.69	0.01	-0.13	-0.55
	30	4.26	0.06	0.62	4.27	0.11	0.72	0.14	0.07	-0.45
	31	4.49	0.05	1.07	4.57	-0.20	0.91	-0.14	-0.34	-0.60
	32	4.44	-0.12	0.60	4.46	-0.08	0.51	-0.10	0.06	0.05
	33	4.41	0.03	0.83	4.47	0.03	0.63	-0.21	0.00	-0.14
	34	4.33	0.05	0.73	4.37	0.18	0.74	0.04	0.17	-0.46
	35	4.51	0.12	1.15	4.60	0.10	0.99	-0.13	-0.03	-0.65
	36	4.53	-0.10	0.80	4.56	0.05	0.90	0.14	0.20	-0.58
	37	4.34	0.02	0.77	4.39	0.15	0.68	-0.07	0.17	-0.45
	38	4.42	0.10	0.91	4.55	0.13	0.58	-0.32	0.03	-0.68
	39	4.52	-0.17	0.82	4.54	-0.00	0.77	-0.03	0.22	-0.23
	40	4.19	0.07	0.67	4.25	-0.04	0.67	0.03	-0.14	-0.64
	41	4.29	-0.19	0.46	4.27	-0.19	0.48	0.02	0.00	0.12
	42	4.39	-0.23	0.68	4.44	-0.07	0.79	0.17	0.21	-0.91

Table 72. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	4.20	-0.10	0.65	4.25	-0.08	0.74	0.15	-0.10	-0.79
	44	4.20	-0.06	0.43	4.22	0.06	0.36	-0.07	0.16	-0.03
	45	4.34	-0.17	0.51	4.37	-0.10	0.36	-0.17	0.09	0.05
	46	4.35	-0.12	0.62	4.43	-0.20	0.58	0.01	-0.11	-0.88
	47	4.35	-0.26	0.50	4.36	-0.30	0.63	0.16	-0.05	-0.43
	48	4.18	-0.03	0.59	4.22	-0.17	0.55	-0.02	-0.19	-0.38
	49	4.21	-0.12	0.50	4.24	-0.08	0.46	-0.02	0.05	-0.29
	50	4.33	-0.14	0.52	4.38	0.08	0.60	0.14	0.30	-0.75
	51	4.35	-0.15	0.78	4.39	-0.26	0.78	0.02	-0.15	-0.41
	52	4.44	-0.27	0.78	4.42	-0.27	0.84	0.06	0.00	0.06
	53	4.34	-0.04	0.89	4.40	-0.17	0.82	-0.04	-0.17	-0.55
	54	4.30	-0.07	0.33	4.32	-0.05	0.44	0.14	0.03	-0.46
	55	4.40	-0.05	0.70	4.42	-0.19	0.83	0.17	-0.19	-0.58
	56	4.48	-0.17	0.61	4.48	-0.22	0.66	0.05	-0.06	-0.03
	57	4.34	0.03	0.64	4.39	-0.17	0.53	-0.10	-0.26	-0.31
	58	4.39	0.04	0.50	4.40	-0.12	0.54	0.06	-0.21	-0.29
	59	4.48	-0.11	0.40	4.48	-0.25	0.46	0.08	-0.19	-0.21
	60	4.43	0.16	0.64	4.51	0.06	0.71	0.15	-0.13	-1.16
	61	4.56	-0.13	0.60	4.60	-0.01	0.57	-0.01	0.16	-0.46
	62	4.44	0.08	0.93	4.48	0.04	0.74	-0.20	-0.06	0.04
	63	4.60	0.20	0.97	4.63	0.05	1.11	0.20	-0.20	-0.78

Table 72. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	4.22	0.16	0.81	4.22	0.02	1.15	0.42	-0.19	-0.95
	65	4.18	0.23	0.79	4.20	0.15	0.95	0.21	-0.10	-0.59
	66	4.45	0.10	0.95	4.49	0.14	1.05	0.16	0.05	-0.69
	67	4.44	0.13	0.97	4.50	-0.01	0.90	-0.03	-0.18	-0.62
	68	4.12	0.27	0.65	4.15	0.13	0.62	-0.01	0.07	-0.31
	69	4.44	0.42	1.31	4.49	0.70	1.64	0.44	0.38	-1.43
	70	4.13	0.04	0.97	4.19	0.09	1.13	0.25	0.07	-1.19
	71	4.35	-0.08	1.02	4.41	0.08	0.97	-0.01	0.22	-0.65
	72	4.28	-0.01	1.01	4.38	0.02	1.04	0.10	0.05	-1.21
	73	4.04	0.12	0.84	4.08	0.27	0.74	-0.10	0.19	-0.23
	74	4.23	0.08	1.11	4.36	0.04	0.88	-0.19	-0.06	-0.87
	75	4.22	-0.15	0.83	4.29	-0.14	0.63	-0.20	0.02	-0.29
	76	4.26	-0.11	1.01	4.35	-0.16	0.88	-0.09	-0.07	-0.73
	77	3.99	0.11	0.72	4.08	0.39	0.69	0.02	0.37	-0.92
	78	4.21	0.02	1.12	4.32	-0.18	0.74	-0.39	-0.27	-0.34
	79	4.30	0.08	0.91	4.36	0.05	0.90	0.03	-0.05	-0.68
	80	4.09	0.18	0.67	4.14	0.15	0.48	-0.19	-0.03	-0.18
	81	4.24	0.14	0.90	4.35	-0.09	0.68	-0.18	-0.31	-0.80
	82	4.13	0.15	0.87	4.20	0.28	0.67	-0.19	0.17	-0.40
	83	4.16	0.10	0.90	4.28	-0.04	0.62	-0.26	-0.19	-0.70
	84	3.98	-0.01	0.85	4.05	-0.15	0.59	-0.28	-0.18	-0.19

Table 73. Genetic effects from Model 1 and Model 2 combined over environments for yield.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	105.31	-9.06	99.21	104.25	3.65	101.05	1.54	16.95	7.66
	2	104.21	1.61	114.69	104.68	0.19	104.26	-12.51	-1.89	21.62
	3	89.92	5.57	112.60	86.83	1.25	120.93	8.11	-5.75	14.79
	4	95.84	-6.74	88.32	96.37	-1.72	89.22	1.49	6.69	-8.62
	5	108.02	-8.17	105.39	108.69	-16.12	115.03	12.34	-10.60	-33.08
	6	100.05	7.80	121.87	102.58	9.80	129.81	11.55	2.66	-50.69
	7	101.74	9.25	86.24	101.62	1.57	73.71	-15.53	-10.24	34.15
	8	104.80	9.95	109.19	105.70	-24.94	142.69	41.90	-46.53	-98.08
	9	108.09	1.32	95.53	103.52	-5.79	92.18	-7.31	-9.47	62.82
	10	105.69	3.75	81.31	105.20	4.28	98.58	20.94	0.71	-39.34
	11	98.71	16.40	95.76	98.89	4.60	99.04	4.16	-15.74	-10.67
	12	96.33	7.20	105.71	100.52	12.88	104.33	1.21	7.57	-45.88
	13	105.27	-3.94	109.54	104.35	3.89	105.83	-5.21	10.45	20.53
	14	108.51	-6.25	105.77	110.45	1.51	108.98	5.30	10.35	-31.33
	15	115.54	11.60	148.51	117.36	30.43	152.33	5.96	25.11	-31.38
	16	90.62	-15.63	89.83	90.27	-13.93	81.84	-10.08	2.26	24.98
	17	96.37	-10.71	101.52	95.39	2.17	91.55	-12.98	17.17	37.69
	18	96.15	-4.06	126.02	96.92	-17.80	120.15	-6.70	-18.33	6.34
	19	96.56	-3.20	75.65	95.89	-9.16	80.69	5.75	-7.95	-5.27
	20	103.00	13.86	115.44	104.19	8.85	127.43	15.60	-6.68	-45.40
	21	92.50	13.47	89.17	93.37	9.62	85.74	-3.62	-5.14	-1.38

Table 73. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	117.16	4.73	107.84	115.32	-4.67	119.02	12.50	-12.54	-7.52
	23	112.05	-6.89	84.32	112.70	-25.97	106.74	28.06	-25.44	-66.13
	24	102.69	14.06	84.49	108.87	-4.81	81.34	0.41	-25.16	-64.88
	25	104.63	1.28	79.50	100.62	-4.11	95.32	16.70	-7.19	6.14
	26	103.57	8.66	90.24	104.92	-6.79	92.17	3.32	-20.59	-21.01
	27	105.55	-13.22	41.99	104.85	-12.75	54.85	15.35	0.63	-25.21
	28	118.80	-5.68	101.23	121.32	-7.25	123.67	24.47	-2.10	-77.91
	29	106.52	15.56	117.78	107.98	18.67	118.25	1.60	4.14	-18.47
	30	115.80	3.10	112.39	114.34	25.27	140.22	33.27	29.56	-55.31
	31	118.79	4.47	131.30	120.88	0.24	146.91	20.68	-5.65	-65.47
	32	127.48	-20.56	108.12	124.12	-23.65	130.21	24.87	-4.12	-17.84
	33	99.96	16.97	99.79	99.91	12.56	118.74	23.30	-5.89	-48.79
	34	114.55	2.66	88.80	116.38	7.64	113.17	31.30	6.64	-85.21
	35	120.72	13.42	123.08	123.53	4.60	124.93	4.25	-11.77	-38.14
	36	123.66	-12.00	84.23	122.19	-6.90	110.59	31.46	6.80	-51.47
	37	99.92	-13.68	106.29	99.45	-3.07	139.05	40.03	14.15	-79.93
	38	104.51	-7.55	130.06	106.87	-12.61	135.53	8.38	-6.75	-42.12
	39	120.92	-32.34	118.75	118.87	-25.63	140.88	25.84	8.95	-33.51
	40	109.90	11.35	108.89	110.89	6.34	128.22	24.51	-6.69	-62.20
	41	114.51	-15.29	74.12	111.16	-18.36	98.92	28.21	-4.09	-24.99
	42	124.53	-27.15	102.59	127.22	-23.30	134.26	40.88	5.14	-114.44



Table 73. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type III										
	43	101.48	-4.96	84.56	101.92	2.62	102.57	22.50	10.11	-52.29
	44	103.50	-11.01	70.76	102.80	0.77	66.51	-5.73	15.71	19.37
	45	119.68	-19.37	90.17	119.78	-12.08	90.32	0.25	9.72	-1.51
	46	116.15	-7.17	103.89	120.27	-15.58	103.85	2.82	-11.22	-48.66
	47	104.51	-2.95	86.79	105.76	8.03	102.47	20.18	14.63	-55.72
	48	86.55	10.34	77.15	89.19	14.80	83.04	9.08	5.94	-46.57
	49	106.05	-5.75	65.20	105.98	-0.99	90.50	31.13	6.35	-65.24
	50	121.91	-10.19	85.44	121.25	4.49	124.68	47.88	19.57	-94.54
	51	114.24	-1.17	96.19	115.29	-12.08	111.19	19.21	-14.54	-51.56
	52	103.90	1.38	79.34	101.00	2.05	80.82	-0.20	0.89	30.46
	53	99.07	15.64	94.05	99.75	14.31	119.61	31.96	-1.77	-74.67
	54	113.77	-7.08	65.02	109.05	-7.28	98.27	37.68	-0.26	-30.90
	55	117.68	2.61	95.08	115.40	-16.16	104.44	9.94	-25.02	2.52
	56	103.55	6.31	64.52	99.50	-1.98	79.11	15.16	-11.05	9.84
	57	105.45	16.05	89.89	106.59	-0.69	97.25	9.87	-22.32	-32.73
	58	131.41	10.24	96.91	133.23	-7.33	90.77	-6.30	-23.43	-5.56
	59	107.36	15.03	53.33	107.75	13.95	69.97	20.77	-1.44	-48.02
	60	112.89	31.98	95.69	113.00	41.13	109.39	16.95	12.20	-37.10
	61	113.48	2.95	88.65	115.49	19.76	95.51	9.86	22.42	-41.71
	62	106.30	16.24	120.29	103.81	17.30	123.53	2.26	1.41	21.07
	63	104.39	10.36	102.30	105.05	-5.71	97.89	-4.98	-21.42	3.72

Table 73. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	81.16	0.64	120.78	79.59	-8.39	134.40	15.69	-12.04	-16.96
	65	79.36	-2.65	104.85	76.51	-8.05	111.91	6.71	-7.20	15.20
	66	110.91	-14.43	151.98	105.16	-7.09	183.76	35.14	9.79	-14.80
	67	104.13	-8.84	136.98	104.12	-15.64	133.06	-4.83	-9.07	10.33
	68	97.05	-15.29	110.80	92.39	-13.65	113.50	0.08	2.18	48.10
	69	107.90	19.86	149.73	116.19	64.72	207.45	76.88	59.82	-248.67
	70	72.71	-4.96	100.37	70.41	2.00	122.07	25.14	9.28	-29.48
	71	105.93	-20.31	136.32	104.82	-15.86	159.55	27.84	5.94	-47.53
	72	101.36	-10.71	128.33	105.12	-12.08	124.06	-2.65	-1.82	-33.26
	73	96.63	-16.80	111.11	97.41	-0.70	112.70	2.50	21.47	-13.40
	74	94.22	-5.90	145.67	96.53	-22.74	161.27	20.82	-22.46	-67.99
	75	105.15	-15.55	106.53	107.67	-22.46	92.92	-15.01	-9.21	5.68
	76	101.14	-10.08	111.24	106.02	-16.69	123.18	18.09	-8.81	-88.83
	77	96.28	-7.84	93.47	99.43	11.98	126.38	42.74	26.43	-123.20
	78	97.24	5.67	143.79	96.02	-5.26	147.67	3.93	-14.58	4.24
	79	117.76	10.57	129.96	117.64	11.35	137.18	8.81	1.03	-17.40
	80	118.33	-1.66	114.47	118.18	-5.40	116.36	2.22	-4.99	-3.22
	81	118.10	16.73	149.30	121.26	4.24	151.37	4.76	-16.65	-42.78
	82	111.07	-6.38	111.85	114.09	3.36	114.10	4.87	12.98	-41.56
	83	100.11	7.77	115.86	108.30	-7.14	111.53	0.36	-19.87	-85.53
	84	97.34	19.94	106.10	101.59	13.41	109.37	7.00	-8.71	-58.85

Table 74. Genetic effects from Model 1 and Model 2 combined over environments for 300-kernel weight.

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type I										
	1	73.07	0.83	14.89	73.81	2.51	15.76	1.58	2.24	-11.00
	2	71.33	0.68	11.17	71.38	2.61	3.95	-8.86	2.57	18.19
	3	67.90	2.80	11.50	68.41	3.72	13.04	2.24	1.23	-10.03
	4	67.04	4.95	12.31	68.48	6.31	12.54	1.28	1.81	-17.60
	5	70.52	-0.35	12.08	70.66	-2.46	14.90	3.58	-2.81	-9.11
	6	75.05	-5.70	17.15	73.95	-7.35	30.90	16.17	-2.20	-22.92
	7	67.57	-1.90	6.24	67.26	-5.55	2.00	-5.44	-4.86	14.70
	8	62.95	3.03	4.47	63.14	0.33	14.13	12.04	-3.59	-27.54
	9	69.72	4.83	15.51	71.41	5.73	6.72	-9.65	1.20	2.89
	10	70.47	0.94	9.73	70.97	4.32	9.01	-0.53	0.51	-4.06
	11	78.11	-5.00	16.92	78.95	-6.26	20.46	4.94	-1.68	-19.16
	12	64.53	3.24	5.25	64.79	1.04	3.93	-1.45	-2.94	0.40
	13	68.86	6.50	18.28	68.81	7.49	20.46	2.64	1.31	-5.11
	14	70.13	0.86	5.04	71.72	1.83	3.66	-0.58	1.29	-15.27
	15	81.53	-5.49	19.38	83.01	-8.26	22.18	4.48	-3.70	-24.85
	16	64.97	1.11	18.54	64.74	1.23	19.24	0.70	0.17	0.90
	17	62.69	-3.26	3.83	61.91	-2.03	3.36	-1.12	1.65	10.43
	18	70.85	-9.23	12.04	69.99	-13.90	17.05	5.56	-6.23	-2.87
	19	65.78	-6.60	10.10	66.69	-10.15	9.95	0.45	-4.73	-10.39
	20	78.60	-10.54	22.32	80.59	-12.88	15.55	-6.95	-3.11	-5.93
	21	77.59	-5.79	18.16	77.08	-8.96	17.48	-1.19	-4.23	7.73

Table 74. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type II										
	22	85.53	-4.42	17.34	84.83	-6.52	26.98	11.40	-2.81	-16.90
	23	80.24	-1.86	12.84	79.44	-2.47	16.27	3.67	-0.81	0.58
	24	83.30	-1.57	16.01	82.79	1.55	14.50	-2.21	4.16	9.95
	25	68.02	8.31	11.87	65.91	9.42	26.31	16.33	1.48	-12.72
	26	78.76	1.88	13.53	78.98	3.73	12.14	-1.56	2.47	1.02
	27	68.67	8.16	5.42	67.63	13.59	6.61	0.74	7.24	9.14
	28	83.82	4.44	11.70	83.00	9.50	19.16	8.63	6.74	-9.77
	29	85.16	2.53	11.57	84.16	5.29	17.88	7.08	3.68	-4.71
	30	74.92	13.76	14.76	73.20	18.62	27.34	14.30	6.47	-12.40
	31	82.84	7.68	16.27	82.27	13.19	23.48	8.49	7.35	-12.12
	32	78.33	12.58	14.26	78.37	19.10	22.86	10.63	8.69	-22.97
	33	80.86	-0.23	8.25	80.02	1.42	9.74	1.26	2.19	5.97
	34	70.52	10.64	9.72	69.28	13.73	14.21	4.67	4.12	2.99
	35	78.50	4.20	11.34	77.30	6.08	10.35	-2.05	2.51	16.75
	36	73.58	9.31	12.44	72.34	13.16	17.59	5.48	5.13	1.32
	37	69.73	10.82	7.38	68.07	11.19	16.31	9.84	0.50	-3.66
	38	76.71	4.00	7.33	75.27	2.46	12.62	5.51	-2.06	3.23
	39	76.37	6.93	12.42	76.35	2.45	15.01	3.17	-5.97	-6.53
	40	63.99	-7.38	6.02	61.58	-9.37	13.84	7.96	-2.65	-8.05
	41	60.24	-3.32	7.62	57.91	-8.45	11.35	2.98	-6.83	17.82
	42	71.07	3.85	8.56	71.94	0.68	15.84	9.57	-4.23	-29.33

Table 74. (Continued)

Type		Model 1			Model 2					
Cross no.		m	a	d	m	a	d	aa	ad	dd
Type III										
43		58.08	7.11	-4.41	55.16	1.65	5.21	9.82	-7.28	9.40
44		59.73	5.52	-9.27	57.94	1.81	-9.39	-1.39	-4.94	21.46
45		63.61	3.80	-4.05	62.32	-2.62	-6.43	-3.83	-8.57	21.47
46		73.82	-1.81	3.57	73.12	-9.49	1.01	-3.63	-10.24	14.93
47		68.11	-4.30	0.73	64.47	-19.02	6.58	4.68	-19.62	27.70
48		71.49	-3.85	-7.25	70.40	-9.39	-8.40	-2.18	-7.38	15.91
49		58.70	-1.39	0.73	59.53	0.34	0.66	0.50	2.31	-9.64
50		61.13	-2.29	7.52	60.44	-1.48	15.93	9.88	1.07	-13.78
51		69.63	-10.86	11.43	69.41	-16.00	15.45	4.80	-6.86	-7.96
52		67.05	-8.28	13.40	64.76	-11.42	16.41	2.12	-4.19	19.24
53		68.45	-11.72	4.78	67.59	-13.64	8.34	3.79	-2.57	0.83
54		62.52	-1.27	4.47	62.77	-1.54	4.36	0.03	-0.36	-2.58
55		70.11	-8.61	9.67	69.48	-15.03	11.77	2.15	-8.56	1.99
56		67.64	-8.34	5.78	67.12	-15.38	11.10	6.19	-9.39	-7.66
57		69.93	-11.19	-1.54	71.01	-15.33	-4.39	-2.75	-5.52	-5.41
58		73.50	-6.63	10.40	74.01	-9.36	1.23	-10.95	-3.64	17.97
59		69.28	-6.42	5.49	69.31	-10.66	8.29	3.47	-5.65	7.68
60		75.07	-7.84	7.61	76.13	-5.06	11.13	5.06	3.70	-21.65
61		80.65	-0.06	15.97	81.12	-0.16	18.32	3.22	-0.13	-11.71
62		80.32	0.54	11.76	79.50	11.07	16.61	5.40	14.03	-2.93
63		82.53	-3.16	18.18	81.58	-1.16	22.90	5.15	2.67	-1.01

Table 74. (Continued)

Type	Cross no.	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dd
Type IV										
	64	73.37	19.48	-9.26	71.22	19.63	2.52	13.01	0.21	-5.27
	65	77.34	14.86	-3.02	74.79	11.87	5.69	8.96	-3.99	7.51
	66	84.20	15.93	7.62	82.08	13.89	19.60	13.29	-2.73	-6.22
	67	85.12	15.15	6.60	83.29	12.98	20.48	15.83	-2.89	-14.55
	68	78.98	19.77	7.32	77.94	19.43	15.24	9.03	-0.46	-8.27
	69	87.51	7.71	1.59	80.31	20.68	28.34	27.95	17.29	15.28
	70	62.77	-0.29	-1.39	62.52	6.61	3.15	5.42	9.21	-8.85
	71	66.33	-3.33	6.49	65.38	-5.80	12.41	6.63	-3.29	-4.19
	72	61.99	-3.94	3.63	59.08	-4.50	16.59	13.93	-0.75	0.65
	73	59.05	2.44	5.23	57.40	3.95	15.26	11.21	2.02	-6.63
	74	69.76	-14.05	-7.39	67.50	-8.14	3.84	12.26	7.89	-2.56
	75	67.76	-0.52	-1.21	68.22	-3.77	-8.90	-9.16	-4.33	14.64
	76	64.69	-1.78	-0.35	62.61	-3.63	14.37	16.68	-2.46	-13.76
	77	61.34	4.49	3.79	60.67	4.98	17.85	16.85	0.65	-28.70
	78	77.31	-12.95	-0.53	76.41	-12.29	7.68	9.49	0.88	-10.81
	79	75.62	-1.27	17.14	74.90	-0.63	19.88	2.88	0.85	1.30
	80	69.56	6.50	12.83	70.45	11.83	13.16	1.04	7.11	-11.38
	81	75.71	-10.49	-3.11	74.33	-4.36	6.15	10.45	8.17	-7.86
	82	74.85	6.02	24.01	75.06	6.20	29.25	6.60	0.24	-16.10
	83	77.57	-9.27	-0.32	76.06	-2.33	11.08	12.99	9.25	-11.88
	84	79.04	-17.71	9.81	78.35	-18.05	6.92	-4.05	-0.45	15.78

Table 75. Standard error of an effect for a given cross combined over environments.

Character	df	Model 1			Model 2					
		m	a	d	m	a	d	aa	ad	dc
Date silk	1121	0.28	0.43	0.86	0.36	0.95	1.48	1.45	1.13	3.55
Plant height	2815	0.90	1.41	2.79	1.18	3.11	4.83	4.73	3.69	11.56
Ear height	2812	0.70	1.09	2.16	0.91	2.40	3.73	3.66	2.85	8.94
Kernel row no.	2645	0.09	0.13	0.27	0.11	0.30	0.46	0.45	0.35	1.10
Ear length	2645	0.13	0.20	0.40	0.17	0.45	0.69	0.68	0.53	1.67
Ear diameter	2645	0.02	0.03	0.06	0.02	0.06	0.10	0.10	0.07	0.23
Yield	2637	1.95	3.05	6.03	2.55	6.71	10.44	10.22	7.97	24.98
300-kernel wt.	2627	0.73	1.14	2.26	0.96	2.52	3.91	3.83	2.99	9.37