

AN INHERITANCE STUDY OF CORN MATURITY

By

CHAMP M. JONES

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**Submitted to the School of Graduate Studies of Michigan
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Department of Farm Crops

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F. L. Rossman

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The inheritance of maturity and ear weight were investigated with six different crosses of early X late inbred lines of corn. Dominance relationships, gene numbers, nature of gene action, and heritability were studied. Silking date, moisture content of ears harvested at a uniform period from time of planting, and ear moisture content fifty days after silking, were used as measures of maturity. Data on ear weight were obtained at two harvest periods.

In each cross, either complete phenotypic dominance or slight heterosis for earliness was indicated in all maturity studies. Some degree of heterosis for earliness was probably involved in each cross; however, the major portion of the observed earliness appeared to be due to dominance of genes for earliness.

Complete genic dominance for early silking, partial to complete genic dominance for lower ear moisture at a uniform harvest period from planting, and variations from none to complete genic dominance for lower ear moisture fifty days after silking were indicated for the crosses. The data suggest that the classification of inbred lines entirely on the basis of silking date may not furnish the desired information on maturation.

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Epistasis for earliness appeared to be exhibited by the dominant genes contributed by the early inbred R53 and possibly by A158. Inbreds containing dominant epistatic genes for earliness should provide more uniformity of maturity in a double cross of the type $(E_1 \times L_1) (E_2 \times L_2)$ than early inbreds with dominant but nonepistatic genes for earliness. Epistasis of dominant genes may aid in explaining reports that crosses of the type $(E_1 \times L_2) \times (E_2 \times L_2)$ were no more variable than that of the type $(E_1 \times E_2) \times (L_1 \times L_2)$.

In the maturity studies, it could not be concluded whether gene action was following either the arithmetic or the geometric schemes. In all cases where calculated means differed from the actual means, the geometric means were closer to agreement with the obtained.

Minimum gene numbers ranged from 5 to 19 for silking data, 2 to 11 for moisture content of ears harvested at a uniform period from planting, and from 1 to 54 for moisture content of ears harvested fifty days after silking.

Maximum heritability values ranged from 11 per cent to 48 per cent for silking date, 36 per cent to 58 per cent for moisture

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content of ears harvested at a uniform period from planting, and 22 per cent to 83 per cent for moisture content of ears harvested fifty days after silking. Heritabilities of ear moisture content averaged higher than heritability of silking date.

Considerable heterosis was exhibited for heavier ear weight in all crosses. Of the early inbreds, R53 was exceptional in its contribution of favorable genes for heavier ear weight. Genes affecting ear weight followed the arithmetic scheme.

Maximum heritability values calculated for ear weight indicated that very little, if any, progress could be expected from selection for heavy ears within the segregating progenies of any of the crosses at the uniform harvest period. However, good progress could be expected from selection within the F_2 generation of the crosses (MS206 X Oh40B), (R53 X W23) and (A158 X W23) in the case of a harvest fifty days after silking.

It was proposed that an F_1 combination of early lines containing dominant epistatic genes with late lines possessing exceptional combining ability for yield may be made as follows:

$$((E_1 \times L_1) E_1) \times ((E_2 \times L_2) E_2).$$

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INTRODUCTION

Corn hybrids adapted to Michigan and other northern areas must be relatively early in maturity in addition to possessing high-yielding ability and other desirable agronomic characters. Under favorable conditions there appears to be a general positive correlation between the lateness of corn varieties and yielding ability (11, 27, 33). Stringfield et al. (33), from a study of the relation between silking date and grain yields in fourteen counties of northern Ohio, showed that a full-season corn hybrid that silks three days later than an earlier hybrid will yield on the average 6 bushels more per acre. Results from hybrid corn trials in Michigan show conclusively that some early-maturing hybrids are capable of yielding as much or more corn per acre than hybrids much later in maturity.

Late-maturing hybrids may not have sufficient time to reach full maturity before killing frost. Rather and Marston (27) reported the loss in yield that may take place due to the cessation in development before maturity. A yield loss of 12 bushels per acre occurred when a late hybrid was harvested at 50 per cent ear moisture compared to harvest at 40 per cent moisture. An

average loss of 0.75 bushels per acre resulted from each day of premature harvest. There are other important advantages in favor of early-maturing hybrids. Lower moisture content of early hybrids at harvest permits safer storage and, in turn, provides better quality feed and less loss from spoilage. Early hybrids may be harvested earlier in the fall, when weather conditions are more favorable and the losses due to stalk breakage and dropped ears may be lower.

In determining the relative maturity of corn hybrids, several different measures have been employed. Some are based on external appearances, such as date of silking, date of tasseling, denting or glazing of kernels, or browning of the plant. Others are based on internal measurements, such as the moisture content of the ear or the translocation of dry matter to the grain. The point at which the maximum amount of dry matter is accumulated in the grain appears to be the best measure of complete maturity; however, it is more difficult to determine.

Studies on the inheritance of quantitative characters present several difficulties as a result of the many genes involved, the small effect of each gene, and the influence of environment on the different genotypes. There are problems of classification

and measurement, and it may be difficult to separate the variability due to environment from that which is due to genetic differences. Some quantitative characters in corn--such as ear length, ear width, ear diameter, plant height, and yield--have received considerably more study than others. There is relatively little information on inheritance of corn maturity, and therefore, more information would be helpful to the plant breeder who is responsible for altering it.

A knowledge of the nature of action and the number of genes controlling the expression of quantitative characters is of value to the plant breeder. They indicate to some extent the possibilities for improvement and aid in the planning of future breeding programs. In making double-cross hybrid predictions of corn yield, method "B" of Jenkins (13) is based upon the assumption of arithmetic gene action. As the number of genes determining a plant character becomes greater, there is less chance of obtaining the desired genes in a single plant, and selection must be practiced from larger populations.

Information on the heritability of a character is important to the plant breeder because it indicates the possibility and extent to which improvement is possible through selection. Wright

(39) defined three types of hereditary or genetic variance: (1) additive genetic variance, (2) variance due to dominance deviation from the additive scheme, and (3) variance due to deviations from the additive scheme resulting from the interaction of nonallelic genes. The additive portion of the genetic variance reflects the degree to which the progeny are likely to resemble the parents. Heritability denotes the additive genetic variance in per cent of the total variance.

The purposes of the present study were to obtain information on dominance relationships, nature of gene action, gene number, and heritability from six different crosses of early X late inbred lines of corn by a study of silking date, moisture content, and ear weight. A study was made of ear moisture content and weight for two different systems of harvesting.

REVIEW OF LITERATURE

The literature available on dominance relations for corn maturity is not in close agreement. In a study of many quantitative characters in corn, Emerson and East (7) crossed two varieties of corn differing in maturity (Tom Thumb pop X Missouri Dent) and found that the F_1 plants were distinctly intermediate in time of anthesis and in time of ripening of the ears. The hardness of the grain and browning of the husk were used as measures of ear maturity. The F_2 generation more than filled the interval between the parents. Eckhart and Bryan (6) indicated that, in crosses between early and late inbred lines of corn, earliness was usually dominant. In four crosses of maize inbreds, Lindstrom (16) found that the F_2 mean was significantly later than the F_1 mean and explained the results on the hypothesis of dominance in genes for fewer days to flowering. Freeman (8) used reciprocal translocations linked with recessive endosperm genes in attempting to locate genes affecting silking date and found no evidence that would indicate dominance of earliness except in one cross. Yang (40) crossed two inbred lines of corn that were approximately equal in maturity and obtained an F_1 generation that

was much earlier in silking date than the parents. It was concluded that heterosis was involved and that dominance of allelomorphs was indicated.

In studying the time-relationships in tassel development of inbred and hybrid corn, Leng (15) divided the period from planting to anthesis into two periods: (1) the period during which the vegetative structures are being initiated up to the elongation of the growing point and (2) the period from elongation of the tassel to anthesis. By comparing the developmental time patterns of three F_1 hybrids and their parental inbreds, a general acceleration of development as a result of heterosis was noted. The mean length of the period between planting and tassel initiation was 4.0 days less in the hybrids than in their inbred parents, while the mean number of days from tassel initiation to anthesis was 3.1 days less in the hybrids.

Dominance relationships on maturity in other crops have been reported by several workers. In crosses between early and late varieties of soybeans, Williams (38), working with an interspecies cross of soybeans, reported that the F_1 was between the parents and that considerable transgressive segregation for maturity occurred in the F_2 . Weiss et al. (37) reported that

maturity date in the F_1 was consistently intermediate between that of the parents in seventeen different soybean crosses. Also working with soybeans, Weber (35) reported that there was a lack of dominance of genes determining maturity and that transgressive segregation occurred in the F_2 and F_3 generations far beyond either parent.

Rasmusson (26) studied the inheritance of quantitative characters in peas. He concluded that there were probably two main genetic factors affecting maturity and that both showed partial dominance for lateness. The two factors appeared to be responsible for about half of the genetic variation within the F_2 population; the other half was due to modifiers and environment.

Powers (22) presented data for tomatoes showing that the period for smaller number of days from seeding to first complete change in color of any fruit was completely dominant in a cross of Danmark X Johannisfeuer in one year and that heterosis was exhibited in the same cross the following year. This evidence was used in support of the hypothesis that heterosis and dominance are dependent upon the same physiological genetic processes. Powers et al. (24) studied three different stages between the time of seeding and first ripe fruit in a tomato cross.

In every period earliness exhibited complete or almost complete phenotypic and genic dominance. Burton (2) found that dominance was indicated for earliness of heading in six different crosses of pearl millet.

There are two types of gene action for quantitative characters that can be distinguished by statistical analysis of the data in inheritance studies: First, there may be no interactions between the genes affecting the quantitative character, in which case the effects of the genes are arithmetically cumulative. This is best illustrated by the work of Mangelsdorf and Fraps (19), who found that in corn the Vitamin A units-per-gram increased approximately 2.25 for each additional Y gene. Secondly, the nature of the interaction of the genes affecting a quantitative character may be such that the effects of the genes are geometrically cumulative (multiplicative). Each gene supposedly multiplies the phenotype by a fixed amount. Charles and Smith (4) and Powers and Lyon (25) presented formulas for the estimation of arithmetic and geometric means.

The author is not aware of any reports of studies of gene action for corn maturity. In a soybean cross, Weber (35) reported that the nature of the gene action for maturity appeared

to be additive. Powers and Lyon (25) in inheritance studies on the duration of developmental stages in tomato crosses, reported about the same values for the arithmetic and geometric means. Burton (2) reported that the calculated arithmetic means for maturity in pearl millet were closer to agreement to the obtained F_2 means in six crosses than were the geometric means.

Freeman (8) made use of reciprocal translocations, linked with recessive endosperm genes *wx*, *su*, and *pr*, to facilitate the identification of plants carrying the translocated chromosomes and to locate genes affecting silking date in inbred lines of corn. It was found that genes for late silking in inbred Florida No. 1 appeared to be located in chromosome 3, in chromosome 5, and in chromosome 8. In inbred Florida No. 2, genes were located the same as in Florida No. 1 and, in addition, were probably located in chromosome 1 and 2. It was concluded that inbred Florida No. 2 had five genes for lateness, and Florida No. 1, only three genes in those portions of the chromosomes examined.

Yang (40), in a study on the nature of genes controlling hybrid vigor as it affects silking time in corn, concluded that the genes involved for hybrid vigor in respect to silking time appeared to be small in number with effects of comparable magnitude

and independently inherited. His conclusion was based on observation of the frequency distribution of the F_2 and reciprocal back-cross generations following a cross of two inbred lines of corn that were similar in maturity.

In an interspecific soybean cross, Weber (35) calculated that only one major gene was differentiating maturity. Goodwin (10) reported that the minimum number of gene substitutions which determine stages of maturity in golden rod was nine. Burton (2) reported that date of heading for six crosses of pearl millet was controlled by a minimum of two to seven genes.

Powers et al. (24) in analyzing data on quantitative characters to ascertain the number of gene pairs differentiating the parents in tomato crosses, used what he termed the partitioning method of analysis. Three genes were found to be differentiating the period from time of seeding to first bloom; three, from first bloom to first fruit set; and two genes, from first fruit set to first fruit ripe.

Information as to the progress to be expected from applying selection pressure to a segregating population is essential in designing a breeding program. In the study of quantitative characters, total variability must be separated into genetic and

environmental variability in order to obtain an estimate of the heritability of a character. Wright (39) outlined procedures for estimating genetic variances and discussed their applications.

Lush (17) described the estimation of heritability from the regression of offspring on the female parent in the case of animals.

Robinson et al. (29), by using data from F_2 parental parent plants and F_3 progeny plots of "biparental" crosses in F_2 populations, obtained three different estimates of heritability for eight different characters in corn. Two of the estimates resulted from parent-offspring regressions, and the third was derived from the components of variance from the analysis of the F_3 progeny data. Heritabilities for plant height, ear height, husk extension, and husk score were relatively high. Those for number of ears per plant, ear length, ear diameter, and yield were considerably lower.

Working with soybeans, Weiss et al. (37) found that single plant maturity determinations were highly indicative of the maturity date of subsequent progenies. This suggested a high degree of heritability. A very high heritability value for maturity in soybeans (86 per cent) was reported by Weber (35).

Mahmud and Kramer (18), in studying segregation following a soybean cross, calculated heritability estimates in three

different ways. Values ranged from 69 to 77 for yield, 74 to 91 for height, and 92 to 100 for maturity when the estimates were based on generations grown in the same season. When different spacings and seasons were involved, heritability estimates were negligible for yield and ranged from 35 to 50 for height and maturity. Burton (2), in studies of pearl millet crosses, obtained relatively high heritability values for maturity.

In examining the literature for dominance relationships in connection with ear dry weight or yield of corn, the problem of heterosis was immediately encountered. In crosses among inbred lines of corn, heterosis of varying degrees for grain yield usually occurs (36, 32, 28).

The nature of the gene action for yield of corn has received considerable study. Neal (20) reported yields for the parents and F_1 and F_2 generation of ten single, four three-way, and ten double crosses. Very close agreement was found between actual and predicted F_2 yields. The predicted F_2 yields were calculated using the formula by Castle and Wright (3), which is based on arithmetic gene action. Kinman and Sprague (14) have presented additional data on the observed and predicted yields of forty-five single crosses and the F_2 generations of these

combinations in which gene action appeared to be predominantly arithmetic. Powers (22) recalculated Neal's data in order to determine whether or not it could also be explained on a geometric hypothesis. However, it was found to agree only with the arithmetic scheme.

Jenkins (13) presented data on the relative efficiency of four methods of predicting the performance of double-cross combinations. The mean value of the four nonparental single-cross combinations gave the best agreement with the actual double-cross performance. This method assumes arithmetic gene action. Other workers found that predicted double-cross performance agreed closely with actual performance (5, 1, 12).

The author did not find any literature reporting the probable number of genes involved in determining ear weight or yielding ability of corn. It is generally believed that numerous genes are involved. Heritability estimates for yield of corn have been reported by Robinson et al. (29). Rather low percentage values (20.1, 9.5, 15.5) were obtained for the three different methods used for estimation.

MATERIALS AND METHODS

Three early and three late inbred lines of corn were used in the six different crosses reported herein. MS206, R53, and A158 were classified as early lines, and W10, Oh40B, and W23 were classified as late. All six lines had been inbred for a long period of time and were of diverse origin. The six different crosses were (MS206 X W10), (MS206 X Oh40B), (R53 X Oh40B), (R53 X W23), (A158 X Oh40B), and (A158 X W23). The data reported were obtained in a field experiment conducted during the summer of 1951 at the Michigan State College Farm Crops farm. All seeds of the different populations were produced in the summer of 1950.

Hereafter, the symbol B_1 is used to signify that the progeny indicated resulted from backcrossing the F_1 generation to the designated parent. P_1 and P_2 are employed to indicate an early or late inbred parent, respectively. For each cross, the experiment included all of the different populations that could be obtained from the two parents and the F_1 generation by crossing and self-pollination: P_1 , B_1 to P_1 , F_1 , F_2 , B_1 to P_2 , and P_2 . A split plot design was used in which the crosses were the main

plots and the generations within each cross were subplots. Eight replications were used. Complete randomization of the main plots and subplots was practiced, except that the two parental inbreds of each cross were grown in adjacent plots. One row each of the P_1 , P_2 , and F_1 and two rows each of the B_1 to P_1 , B_1 to P_2 , and F_2 generations constituted a plot. Each row consisted of twenty-five hills spaced 1 foot apart. Two seeds per hill were planted on May 19. When the average height of the seedlings was approximately 1 foot, the plants were thinned to one stalk per hill in such a manner as not to bias the results of the experiment. A good stand was obtained for all of the populations.

Weather conditions were generally unfavorable during the latter part of the growing season for normal maturity of corn. The latter part of August and the major part of September were cloudy, cool, and wet. Killing frost occurred on September 29, 133 days after planting.

Each plant was tagged for silking date when the silk of the main ear was approximately one-half inch in length. Complete coverage of the experiment was made each day during the period of most rapid silking and on alternate days during periods

of infrequent silking. Dates of silking were transformed to values for the number of days from planting to silking.

Before harvest, plants which were noticeably damaged by insects or diseases were excluded. Two different harvesting systems were used. Six replications of the experiment were harvested at a uniform time from planting (September 18 to 21)--when the more advanced ears appeared to have matured satisfactorily so that a rather wide moisture content between populations of the crosses would be obtained. The time of harvest was before frost and approximately fifty days after 50 per cent of the plants in the entire experiment had silked. A second system of harvesting was followed with two adjacent replications where each ear was harvested exactly fifty days after silking. In both systems, harvest was accomplished by husking the ear of each plant and placing the ear and silking date tag in a paper bag marked with row and plant number. The paper bag had small holes to facilitate air movement in drying. Green weight in grams for each ear was recorded soon after harvest.

After drying to constant weight in a steel oven set at approximately 155° F., the dry weight of each ear was determined. The ovens reduced the moisture content of the ears to 2 per cent;

proper adjustments were made for the moisture data reported.

Data on ear weight are reported as oven-dry weight, containing approximately 2 per cent moisture. In discussing the data on ear weight, the term "dry weight" is used in this study, even though the weights are actually oven-dry weights.

Means and variances were calculated from individual plant data in all cases. In the calculation of the total population variances, the effect of replication was removed. The significance of means was tested by the standard "t" test (31).

Because of the large environmental variability among the parent lines for silking date and moisture content, the variance of the F_1 was used as an estimate of environmental variance for the segregating generations of each cross. The within generation variance of the F_1 population was subtracted from that of the F_2 , B_1 to P_1 , and B_1 to P_2 generations in estimating the genetic variance of the respective populations.

Formulas reported by Powers and Lyon (25) were used to calculate the theoretical means to determine whether the nature of gene action was more nearly arithmetic or geometric. These formulas are shown in Table 1.

TABLE 1

FORMULAS FOR ESTIMATING ARITHMETIC AND GEOMETRIC MEANS

Population	Arithmetic Mean	Geometric Mean
F_2	$\frac{\bar{P}_1 + 2\bar{F}_1 + \bar{P}_2}{4}$	Antilog of $\frac{\text{Log } \bar{P}_1 + 2\text{Log } \bar{F}_1 + \text{Log } \bar{P}_2}{4}$
$B_1 \text{ to } P_1$	$\frac{\bar{F}_1 + \bar{P}_1}{2}$	Antilog of $\frac{\text{Log } \bar{F}_1 + \text{Log } \bar{P}_1}{2}$
$B_1 \text{ to } P_2$	$\frac{\bar{F}_1 + \bar{P}_2}{2}$	Antilog of $\frac{\text{Log } \bar{F}_1 + \text{Log } \bar{P}_2}{2}$

* \bar{P}_1 , \bar{F}_1 , and \bar{P}_2 represent the mean of the early parent, F_1 , and late parent, respectively.

To test the agreement between observed and calculated arithmetic or geometric means of the F_2 and backcross populations, the analysis of variance was used. Degrees of freedom for the analysis of variance for each comparison between the six obtained and calculated means for the F_2 , B_1 to P_1 , or B_1 to P_2 populations were as follows:

Source of Variation	Degrees of Freedom
total	11
between means	1
between crosses	5
error (crosses x means)	5

The formula supplied to Burton (2) by Sewall Wright was used to estimate the minimum number of genes controlling the expression of a single character. An error was made in the printing of the formula in that the variance of the mean of the F_2 and F_1 in the denominator of the formula should have been the variance of the F_2 and F_1 populations. The formula as used was as follows:

$$N = \frac{0.25 (0.75 - h + h^2) D^2}{\sigma^2_{F_2} - \sigma^2_{F_1}} \quad \text{where}$$

$$h = \frac{\bar{F}_1 - \bar{P}_1}{\bar{P}_2 - \bar{P}_1}, \quad D = \bar{P}_2 - \bar{P}_1,$$

\bar{P}_1 = the mean of the smaller parent

\bar{P}_2 = the mean of the larger parent

\bar{F}_1 = the mean of the F_1 population

\bar{F}_2 = the mean of the F_2 population

According to Burton (2), this formula will furnish an unbiased estimate of the gene number if the following assumptions apply:

1. no linkage exists between pertinent genes,
2. one parent supplies only plus factors and the other only minus factors among those in which they differ,
3. all genes are equally important,
4. the degree of dominance of all plus factors is the same for all,
5. no interaction exists between pertinent nonallelic genes.

When these assumptions do not apply, the formula gives a value that may be much smaller than the true gene number.

Estimates of heritability for each cross were made by the formula, $\text{Variance } F_2 - \text{Variance } F_1 / \text{Variance } F_2$, where the variance in each case represented the total population variance with the effect of replication removed.

As pointed out by Wright (39), the use of the difference between the variance of the F_2 and F_1 as an estimate of genetic variance is actually an estimate of the sum of the following variances:

1. Total genetic variance including:
 - a. additive genetic variance,
 - b. variance due to dominance deviations from the additive scheme,
 - c. variance due to the interaction of nonallelic genes.
2. Variance due to interaction of the genotypes and the environment.

Thus, the estimates obtained must be considered as maximum heritabilities because the additive part of the total genetic variance is the only portion considered heritable.

EXPERIMENTAL RESULTS ON CORN MATURITY

Days From Planting to Silking

Means, standard deviations, and total and genetic variances for the number of days from planting to silking for populations of the six different crosses are shown in Table 2. Frequency distributions and the total number of plants in each population are presented in Table 3. In Table 2 it can be observed that the total variances of the inbred parents in most cases were large. The inbreds were affected more by environment than the F_1 . Thus, the variance of the F_1 population was used as an estimate of environmental variance in the calculation of genetic variances.

Dominance relationships. In the study of dominance relationships, both genic and phenotypic dominance (9, 23) are considered. Genic dominance denotes the degree of expression of one or the other of the two contrasted alleles of the heterozygous gene pair (Aa) plus the action of the environment, in which A represents any gene and a its allele. Thus, an intra-allelic interaction of A and a may be involved as well as an interaction with the environment. Phenotypic dominance denotes the degree of

TABLE 2

MEANS AND THEIR STANDARD DEVIATIONS, TOTAL AND
GENETIC VARIANCES FOR NUMBER OF DAYS
FROM PLANTING TO SILKING

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
MS206 x W10				
MS206	72.8	0.35	16.90	
B ₁ to MS206	71.4	0.17	10.77	- 0.64
F ₁	73.3	0.25	11.41	
F ₂	76.2	0.21	16.81	5.40
B ₁ to W10	80.3	0.25	20.91	9.50
W10	92.2	0.33	15.00	
MS206 x Oh40B				
MS206	72.1	0.32	15.41	
B ₁ to MS206	68.9	0.16	8.13	0.92
F ₁	71.0	0.20	7.21	
F ₂	72.6	0.20	13.98	6.77
B ₁ to Oh40B	77.0	0.22	17.49	10.28
Oh40B	85.0	0.32	13.75	
R53 x Oh40B				
R53	73.9	0.24	10.29	
B ₁ to R53	70.7	0.14	7.34	- 2.22
F ₁	72.4	0.23	9.56	
F ₂	73.6	0.18	11.25	1.69
B ₁ to Oh40B	75.6	0.17	11.34	1.78
Oh40B	85.4	0.35	17.57	

TABLE 2 (Continued)

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
R53 x W23				
R53	73.4	0.22	7.95	
B ₁ to R53	70.4	0.15	7.53	- 3.32
F ₁	73.5	0.25	10.85	
F ₂	74.7	0.20	15.28	4.43
B ₁ to W23	76.2	0.19	13.37	2.52
W23	86.8	0.31	16.46	
A158 x Oh40B				
A158	76.3	0.28	12.73	
B ₁ to A158	73.9	0.17	10.16	1.24
F ₁	74.2	0.23	8.92	
F ₂	75.1	0.21	14.63	5.71
B ₁ to Oh40B	78.4	0.21	15.95	7.03
Oh40B	86.6	0.33	15.51	
A158 x W23				
A158	75.3	0.28	12.48	
B ₁ to A158	72.3	0.14	7.17	- 3.24
F ₁	73.3	0.26	10.41	
F ₂	73.3	0.19	11.75	1.34
B ₁ to W23	77.5	0.20	14.24	3.83
W23	85.6	0.28	11.89	

TABLE 3

FREQUENCY DISTRIBUTION FOR NUMBERS OF DAYS FROM
PLANTING TO SILKING FOR POPULATIONS OF CORN CROSSES

Popu- lation	Number of Days from Planting to Silking																					
	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	
MS206 x W10																						
MS206			1	5	5	8	15	9	4	18	18	17	6	8	4	6	4	1	1	2	3	
B ₁ to]																						
MS206]	1		2	10	18	32	56	36	27	72	42	23	10	13	2	4	6	1		2	5	
F ₁					1	2	18	16	16	31	25	19	7	16	11	3	3	2	3	3	1	
F ₂			2	1	2	7	16	9	33	37	39	28	57	31	25	14	13	19	11	12		
B ₁ to]																						
W10]								1	2	5	13	17	16	21	29	24	21	23	38	35	31	
W10																					1	
MS206 x Oh40B																						
MS206		1	3	8	8	5	20	11	5	26	18	13	6	5	3	7	5		3	1	2	
B ₁ to]																						
MS206]	3	8	22	43	31	45	47	46	7	21	19	15	3	6			1			1		
F ₁			2	5	8	16	29	32	11	29	17	14	5	7	4	1	1					
F ₂	1		1	10	10	12	26	44	5	60	53	42	19	21	4	5	7	7		1	2	
B ₁ to]																						
Oh40B]						1	3	5	25	37	38	48	45	23	42	25	22	15		18		
Oh40B															1	3	5	4	18	2	19	
R53 x Oh40B																						
R53					4	3	10	27	28	22	22	11	13	13	6	6	3	1	3	1		
B ₁ to]																						
R53]		3	8	27	38	54	52	49	70	18	17	9	10	3	3		1			1		
F ₁					1	5	20	34	9	40	22	13	11	7	4	3	3	2	3		1	
F ₂					3	12	13	37	16	59	64	51	24	31	13	14	6	7	3	2	2	
B ₁ to]																						
Oh40B]						3	11	3	31	56	44	48	77	21	31	24	6	5	7	5		
Oh40B																	3	7	10	8	5	24

TABLE 3 (Continued)

Number of Days from Planting to Silking																				Total
84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	
MS206 x W10																				
1																				136
1																				363
1				1																179
8	4	6	3	1				1												379
11	9	13	12	12	2	2	2	1		1	1						1			343
1	2	3	10	10	14	9	10	13	6	21	15	5	7	6	1	2	2		1	139
MS206 x Oh40B																				
																				150
																				318
																				181
1	3			1			1													336
2	6	1	4	1	3		1		1	1		1	1							369
7	21	5	21	2	19	1	4	3			1		1							137
R53 x Oh40B																				
			1	1																175
						1														364
	1																			179
2		1			1						1									362
	2	1			1	1			2					1						380
2	24	3	25	3	15	1	4	1	2	3	2		1	1		1				145

TABLE 3 (Continued)

Popu- lation	Number of Days from Planting to Silking																					
	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	
R53 x W23																						
R53				1		1	5	11	7	19	28	23	26	12	12	13	2	3	2	2		
B ₁ to] R53]				5	11	23	36	63	60	36	35	17	20	7	3	1	2	1	1		4	1
F ₁						4	5	10	15	21	30	23	16	17	7	10	8	4	1	4	1	2
F ₂				2	2	5	27	17	20	61	38	38	34	33	23	17	13	13	8	6	4	
B ₁ to] W23]				1			2	4	18	32	31	52	41	47	28	23	18	10	16	8	17	
W23															1		6	2	6	6	23	
A158 x Oh40B																						
A158										7	15	14	21	20	15	16	9	13	6	7	4	3
B ₁ to] A158]				1		3	15	21	35	61	53	48	34	29	17	10	5	4	2	6	2	
F ₁						4	6	18	24	28	22	16	12	12	9	2	4	1	4			
F ₂				1	1	1	4	9	13	12	49	31	42	39	44	14	21	15	9	5	6	10
B ₁ to] Oh40B]								1	3	9	17	19	29	56	43	49	48	19	17	10	19	
Oh40B																2	4	4	7	2	19	
A158 x W23																						
A158						3	2	12	18	18	27	16	12	19	6	4	5	7	2	3		
B ₁ to] A158]				1		5	10	29	39	60	72	39	38	17	17	15	4		3	2	1	2
F ₁						2	8	16	20	39	14	14	10	8	9	5	2	3	2	2	1	
F ₂				3	5	7	23	28	31	60	44	38	23	22	20	13	6	8	2	4	1	
B ₁ to] W23]						1			8	12	20	31	42	55	42	28	27	10	22	12	14	
W23																3	3	1	10	10	13	

TABLE 3 (Continued)

Number of Days from Planting to Silking																			Total		
84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103		
R53 x W23																					
3																			170		
1																			327		
2																			180		
5	4		1	3	1	1	2		1											379	
1	2	2	2		2	1	1			1						1					361
7	26	16	17	9	8	5	10	8	2	8	3	1	1	2				1	1		169
A158 x Oh40B																					
2	3		1	1															157		
4	3	1	1																	355	
1		1																		164	
2	6	1	2																	337	
5	11	2	9	2	3	2	2		1		1					1					378
2	21	4	25	3	22		5	3	8	1	4				1	2					139
A158 x W23																					
2		2		1															159		
																				354	
1		1																		157	
2		1			1															342	
7		4	5	5	1	4	1													351	
4		13	20	17	11	10	4	7	3	4	1										154

expression of one or the other of two contrasted characters in the F_1 generation as compared to the expression in the two parents; therefore, both intra-allelic and interallelic interactions may be involved, as well as interactions between the genes and environment.

The following theoretical situations were used as guides in the interpretation of dominance relations. No (intermediate) phenotypic dominance is indicated when the F_1 mean for a character equals the average of the means of the two parents. If genic dominance is also intermediate and there is no interallelic interaction of genes, the F_2 mean would not be expected to deviate significantly from the F_1 mean, and the mean of each backcross would be expected to fall half-way between the F_1 mean and the mean of the parent to which the backcross was made.

Complete phenotypic dominance is indicated when the F_1 mean does not differ significantly from the mean of one of the parents in the cross. The F_2 mean would be expected to fall between the two backcross means and should differ significantly from the F_1 mean. The mean of the backcross to the dominant parent should not differ significantly from the mean of the F_1 or dominant parent. The mean of the backcross to the recessive

parent should fall between the mean of the F_1 and the recessive parent but closer to the mean of the F_1 .

Partial phenotypic dominance is indicated when the F_1 mean falls between the mean of one of the parents and the average of the two parental means. The F_2 mean should fall between the two backcross means and should more nearly approach the mean of the F_1 as the degree of dominance becomes less.

In determining genic dominance, the calculated genetic variances of the segregating populations were used. Complete genic dominance is indicated when the genetic variance of the backcross to one parent is negligible and that of the F_2 and backcross to the other parent is large. Intermediate (no) genic dominance is indicated if the genetic variances of the two backcross populations are approximately equal. Any situation not falling into the category of complete or intermediate genic dominance would be partial genic dominance.

Heterosis is exhibited when the F_1 mean for a character falls significantly beyond the mean of either parent of a cross. If the F_1 generation shows heterosis, the backcross to the parent more closely approaching the F_1 should also exhibit heterosis.

The F_2 mean should fall half-way between the mean of the F_1 and the average of the two parents.

As used in the present studies, the term "epistasis" refers to the interallelic interaction of genes in which a dominant gene of one allelic pair tends to mask the effects of double recessive genes of other allelic pairs affecting the same character. If complete epistasis is involved, one dominant gene produces as great an affect as all other dominant genes affecting the character in a genotype. When epistasis, phenotypic dominance, and genic dominance are complete, very small differences should be observed between the means of the dominant parent, backcross to the dominant parent, F_1 , F_2 , and backcross to the recessive parent. With complete phenotypic and genic dominance and no epistasis, the means of the F_2 and backcross to the recessive parent should deviate significantly from the F_1 mean--the degree of deviation depending considerably upon the number of genes affecting the character. Different degrees of epistasis may be indicated when the situation suggests neither complete, nor the absence of, epistasis.

A summary of the dominance relationships for the number of days from planting to silking is presented in Table 4. The

TABLE 4

SUMMARY OF DOMINANCE RELATIONSHIPS FOR NUMBER OF
DAYS FROM PLANTING TO SILKING FOR CORN CROSSES

MS206 x W10

Complete phenotypic
dominance
Complete genic dominance
No epistasis

MS206 x Oh40B

Slight heterosis
Complete genic dominance
No epistasis

R53 x Oh40B

Slight heterosis
Complete genic dominance
Strong epistasis

R53 x W23

Complete phenotypic
dominance
Complete genic dominance
Partial epistasis

A158 x Oh40B

Slight heterosis
Complete genic dominance
Possible epistasis

A158 x W23

Slight heterosis
Complete genic dominance
Possible epistasis

dominance relationships of the crosses were generally similar. In the cross (MS206 X W10), the F_1 mean did not differ significantly from that of MS 206 (Table 2), so that complete phenotypic dominance was indicated for earliness of silking. Complete genic dominance was indicated by the negative estimated genetic variance of the backcross to MS206 and by the relatively large genetic variance of the F_2 and the backcross to W10. The mean of the backcross to MS206 was significantly less than that of the F_1 and MS206--indicating that intra-allelic and interallelic gene interactions must have occurred. Epistasis of the early silking dominant genes did not appear to be involved, as evidenced by the fact that the means of the F_2 and backcross to W10 were considerably greater than that of the F_1 .

Slight heterosis was exhibited in the cross (MS206 X Oh40B) since the mean of the F_1 was significantly less than that of MS206. Almost complete genic dominance for earliness of silking was indicated in that the estimated genetic variance of the backcross to MS206 approached zero and was small in comparison to that of the F_2 and the backcross to Oh40B. Probably no epistasis of dominant genes occurred, since the mean of the backcross to Oh40B was considerably larger than that of the F_1 or the F_2 .

In the cross (R53 X Oh40B) the means of the F_1 and the backcross to R53 were both significantly less than the mean of R53. Definite heterosis was exhibited. The negative genetic variance calculated for the backcross to R53 suggested that complete genic dominance was involved for earliness of silking. In this cross it appeared that dominant genes for early silking were epistatic to double recessive genes, since there were small differences between the means of the F_1 , F_2 , and backcross to Oh40B. The low genetic variances estimated for the F_2 and backcross to Oh40B further support the hypothesis of epistasis. Segregation for early silking beyond that of R53 or the F_1 occurred in the backcross to R53 (Table 3), indicating intra-allelic and interallelic gene interactions.

Complete phenotypic dominance was indicated for the cross (R53 X W23), because the mean of the F_1 did not differ significantly from the mean of R53. The negative genetic variance of the backcross to R53 indicated complete genic dominance for earliness of silking. The genetic variances calculated for the F_2 and backcross to W23 populations were rather low but were larger than that calculated for the backcross to R53. Some degree of epistasis of dominant genes for early silking seemed probable

in this cross, because there were small differences between the means of the first five populations. The frequency distribution (Table 3) supports the hypothesis of possible epistasis, since there was very little segregation for late silking in the F_2 and B_1 to W23, beyond that of the F_1 .

Slight heterosis for earliness of silking was indicated in the cross (A158 X Oh40B) in that the mean of the F_1 was significantly less than that of A158. A high degree of heterosis did not occur, since the F_2 mean fell closer to that of the F_1 than would have been expected. There was almost complete genic dominance for earliness of silking as shown by the small genetic variance of the backcross to A158, when compared with that of the F_2 or the backcross to Oh40B. The mean of the backcross to Oh40B fell somewhat closer to the mean of the F_1 than to that of Oh40B, supporting the hypothesis of dominance of genes for early silking. Some degree of epistasis was indicated by the closeness of the F_1 and F_2 means. However, the relatively large difference between the mean of the F_1 and B_1 to Oh40B suggested that epistasis may not have been involved.

Heterosis for early silking was exhibited by the cross (A158 X W23) since the F_1 was earlier than the inbred A158. The

fact that there was no difference between the F_2 and F_1 means suggests that a high degree of heterosis was not involved. Complete genic dominance was indicated by the highly negative genetic variance calculated for the backcross to A158. The genetic variances estimated for the F_2 and B_1 to W23 populations were rather small, but larger than that of the backcross to A158. Since the mean of the backcross to W23 was significantly larger than the mean of the F_1 , epistasis was not apparent. However, the equal F_2 and F_1 means indicated epistasis.

In all of the crosses, either complete phenotypic dominance or slight heterosis was noted for earliness of silking. Complete, or almost complete, genic dominance was also indicated in every cross. The backcross to the early parent was significantly earlier in silking than the F_1 or the early parent in all crosses except (A158 X Oh40B). In backcross populations to the early parent, slight segregation for early silking beyond that of the F_1 or early parent was obtained in every cross--more noticeably in the crosses (R53 X Oh40B), (A158 X Oh40B), and (A158 X W23) (Table 3). It would appear that intra-allelic and interallelic gene interactions must have occurred to give the observed results for the backcrosses

o the early parent. However, some degree of heterosis was also probably involved.

Nature of gene action Calculated means based on the assumption of arithmetic and geometric gene action for the F_2 and backcross populations of each cross are presented in Table 5. In all cases the obtained means were less than either calculated mean, indicating dominance for early silking in all crosses. Because there was very little difference between the mean of the F_1 and that of the early parent of each cross, the arithmetic and geometric means of the B_1 to P_1 populations were the same. In the F_2 and B_1 to P_2 populations, the calculated geometric means were slightly less in every case than the calculated arithmetic means. However, there was very little difference between the two.

An analysis of variance was made to determine the agreement between the obtained means and those calculated on the assumption of arithmetic or geometric gene action. From the F values reported in Table 5, it was evident that the mean of the obtained means for the F_2 and the two backcross populations for all crosses was significantly different from that of the arithmetic or geometric means. However, the mean of the geometric means

TABLE 5

OBTAINED AND CALCULATED ARITHMETIC AND GEOMETRIC MEANS FOR NUMBER OF DAYS FROM PLANTING TO SILKING

Cross	F ₂ Population		
	Obtained Mean (days)	Calculated Mean	
		Arith- metic (days)	Geo- metric (days)
MS206 x W10	76.2	77.9	77.5
MS206 x Oh40B	72.6	74.8	74.6
R53 x Oh40B	73.6	76.0	75.8
R53 x W23	74.7	76.8	76.6
A158 x Oh40B	75.1	77.8	77.7
A158 x W23	73.3	76.9	76.7
Mean	74.3	76.7	76.5
F value		85.8**	59.9**

** Significant at the 1% level

TABLE 5 (Continued)

B ₁ to P ₁ Population			B ₁ to P ₁ Population		
Obtained Mean (days)	Calculated Mean		Obtained Mean (days)	Calculated Mean	
	Arith- metic (days)	Geo- metric (days)		Arith- metic (days)	Geo- metric (days)
71.4	73.1	73.1	80.3	82.8	82.2
68.9	71.6	71.6	77.0	78.0	77.7
70.7	73.2	73.2	75.6	78.9	78.6
70.4	73.5	73.5	76.2	80.2	79.9
73.9	75.3	75.3	78.4	80.4	80.2
72.3	74.3	74.3	77.5	79.5	79.2
71.3	73.5	73.5	77.5	80.0	79.6
	71.3**	71.3**		32.6**	24.4**

for the F_2 and B_1 to P_2 populations was slightly closer to agreement with the obtained than the mean of the arithmetic means.

It cannot be concluded that the genetic variability in the crosses studied was following either the arithmetic or the geometric scale. Both types of gene action may have been involved in all of the crosses.

Gene number and heritability The formula used for the calculation of gene number and the assumptions involved are presented in the section on Materials and Methods. It could not be determined how well the data fit all the assumptions on which the formula is based. The assumption of no interactions between non-allelic genes probably was not valid in the crosses involving R53 and W23 because of the epistasis which appeared to exist. Some gene interactions most likely occurred in all crosses because the observed means failed to fit the calculated arithmetic means. It should be remembered that when the assumptions do not apply the formula gives a value that may be much smaller than the true gene number. The assumption that one parent supplies only plus factors and the other only minus factors among those in which they differ appeared to be quite true because of the relatively small amount of segregation beyond the extremes of the parents.

Results of the calculation of minimum gene numbers for the different crosses are shown in Table 6. Lowest gene numbers were calculated for the crosses (A158 X Oh40B), (MS206 X Oh40B), and (R53 X W23). Selection for maturity based on date of silking should be more successful in the crosses with the smaller gene number. It can be noted from the frequency distributions (Table 3) that better recovery of the extremes in silking of the late parents was obtained in the F_2 and the B_1 to P_2 population in those crosses for which the lower gene numbers were calculated. Recovery of early silking was good in all crosses regardless of gene number.

Estimated heritability values are presented in Table 6. The reported values are considered as a maximum because the genetic variance used in the formula included variability due to dominance, nonallelic gene interactions, interactions of the genotypes and the environment, in addition to additive genetic variance. Highest heritability values were obtained for the crosses (MS206 X Oh40B) and (A158 X Oh40B). As expected, heritability values for the crosses (R53 X Oh40B) and (A158 X W23) were rather low because the gene numbers in both crosses were relatively high. Heritability of 48 per cent for the cross (MS206 X Oh40B) suggested

TABLE 6

ESTIMATED GENE NUMBER AND HERITABILITY VALUES FOR
NUMBER OF DAYS FROM PLANTING TO SILKING

Cross	Minimum Gene Number	Maximum Heritability (%)
MS206 x W10	12.6	32
MS206 x Oh40B	5.2	48
R53 x Oh40B	17.6	15
R53 x W23	7.5	30
A158 x Oh40B	4.6	39
A158 x W23	19.4	11
Mean		29

that considerable progress in altering silking date by selection could be made within segregating progenies similar to the F_2 generation studied. The low genetic variance of the backcross to the early parent in all crosses indicated that very little, if any, progress in altering silking date by selection could be made within these progenies. However, considerable progress could be made within the backcross populations to the late parent because of the relatively large genetic variances obtained.

Moisture Content of Ears Harvested at a Uniform Period From Date of Planting

Six replications of the experiment were harvested approximately fifty days after half of the plants in the experiment had silked and before frost had occurred. Shaw and Thom (30) showed that double-cross corn hybrids reached maturity approximately fifty days after silking. If this condition is generally true for all corn, then it would be expected that approximately half of the ears in this harvest would have reached maturity at the time of harvest indicated.

Means, standard deviations, and total and genetic variances for moisture content of ears harvested at a uniform period from

planting for the six crosses are reported in Table 7. Frequency distributions for the populations are reported in Table 8.

Dominance relationships. A summary of the dominance relationships for moisture content of ears harvested at a uniform period from planting is given in Table 9. In the cross (MS206 X W10), the mean of the F_1 (Table 7) was slightly less but not significantly different from the mean of MS206, indicating that complete phenotypic dominance existed for a lower percentage of ear moisture. The mean of the backcross to MS206 was significantly less than that of the F_1 . Considerable genetic variance was estimated for the B_1 to MS206 population. However, it was much less than that of the F_2 and backcross to W10. Thus, partial genic dominance was indicated for the genes affecting a lower percentage of moisture. The mean of the F_2 fell between that of the backcrosses and deviated considerably from the mean of the F_1 , indicating that there was probably no epistasis of dominant genes. Slight segregation occurred in the F_2 and B_1 to MS206 (Table 8) for a lower moisture percentage beyond MS206 and the F_1 , showing that intra-allelic and interallelic gene interactions were probably involved. In this cross (MS206 X W10) the dominance relationships

TABLE 7

MEANS AND THEIR STANDARD DEVIATIONS, TOTAL AND GENETIC VARIANCES FOR MOISTURE CONTENT OF EARS HARVESTED AT A UNIFORM PERIOD FROM PLANTING

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
MS206 x W10				
MS206	43.4	0.44	19.99	
B ₁ to MS206	41.1	0.27	19.81	6.02
F ₁	42.6	0.32	13.79	
F ₂	47.1	0.34	32.61	18.82
B ₁ to W10	53.8	0.41	44.36	30.57
W10	75.3	0.64	46.62	
MS206 x Oh40B				
MS206	41.8	0.34	12.76	
B ₁ to MS206	40.4	0.24	13.85	5.68
F ₁	42.5	0.24	8.17	
F ₂	44.2	0.28	19.64	11.47
B ₁ to Oh40B	50.2	0.34	33.36	25.19
Oh40B	60.5	0.56	32.13	
R53 x Oh40B				
R53	47.8	0.32	14.36	
B ₁ to R53	43.0	0.16	7.33	- 3.72
F ₁	44.9	0.28	11.05	
F ₂	46.2	0.25	17.29	6.24
B ₁ to Oh40B	48.3	0.26	19.99	8.94
Oh40B	61.0	0.55	33.39	

TABLE 7 (Continued)

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
R53 x W23				
R53	47.8	0.33	14.78	
B ₁ to R53	42.2	0.22	12.33	- 4.58
F ₁	43.9	0.35	16.91	
F ₂	46.0	0.36	36.53	19.62
B ₁ to W23	45.6	0.35	33.23	16.32
W23	62.4	0.92	112.00	
A158 x Oh40B				
A158	49.0	0.41	20.71	
B ₁ to A158	47.4	0.28	20.52	6.53
F ₁	47.9	0.33	13.99	
F ₂	49.2	0.30	22.71	8.72
B ₁ to Oh40B	53.2	0.31	27.01	13.02
Oh40B	61.8	0.54	30.90	
A158 x W23				
A158	49.0	0.40	18.95	
B ₁ to A158	44.4	0.22	12.90	- 0.28
F ₁	44.9	0.33	13.18	
F ₂	45.5	0.32	25.89	12.71
B ₁ to W23	49.4	0.35	31.75	18.57
W23	58.2	0.87	94.22	

TABLE 8

FREQUENCY DISTRIBUTION FOR MOISTURE CONTENT OF
EARS HARVESTED AT A UNIFORM PERIOD FROM DATE
OF PLANTING FOR POPULATIONS OF CORN CROSSES

Popu- lation	Class Centers for Per Cent Moisture													
	32	34	36	38	40	42	44	46	48	50	52	54	56	58
MS206 x W10														
MS206			3	10	20	22	17	8	7	7	4	2		1
B ₁ to]														
MS206]	3	12	29	46	63	41	31	25	8	7	2	1	2	1
F ₁		2	4	17	31	26	19	20	8	2		3	1	1
F ₂	2	1	8	6	19	28	37	57	38	29	14	12	11	7
B ₁ to]														
W10]					2	11	6	17	26	27	33	28	35	20
W10														1
MS206 x Oh40B														
MS206	1	1	8	13	23	22	22	11	5	2	3			
B ₁ to]														
MS206]		5	23	67	53	49	22	13	3	3		2		1
F ₁			1	15	30	38	31	14	5		4		1	
F ₂			2	7	40	57	61	38	16	9	11	2		3
B ₁ to]														
Oh40B]					1	9	28	49	48	45	44	19	12	9
Oh40B										1	5	8	25	10
R53 x Oh40B														
R53			1		4	11	16	29	24	19	15	9	4	3
B ₁ to]														
R53]		1	9	17	41	66	73	44	14	9	1		1	
F ₁				1	13	23	44	26	13	6	6	3	2	
F ₂			3	4	16	34	60	65	33	19	16	12	6	3
B ₁ to]														
Oh40B]					8	18	45	57	49	35	39	13	11	6
Oh40B										1	6	10	14	16

TABLE 8 (Continued)

Class Centers for Per Cent Moisture															Total
0	62	64	66	68	70	72	74	76	78	80	82	84	86	88	
MS206 x W10															
1															102
1		1	1												274
															134
6	5	4													285
7	11	7	9	5			2			1			1		258
3	2	5	4	10	6	10	5	13	15	14	6	14	5	1	114
MS206 x Oh40B															
															111
		1													242
															139
		1		1			1								249
9		3	1	1	3		1	1				1			284
9	12	6	12	4	5	2	2	1			1				103
R53 x Oh40B															
1	1														137
															276
															137
		1	1			1									274
4	1			1	1		1								289
3	12	8	9	8	8	4	1	1	1						112

TABLE 8 (Continued).

Popu- lation	Class Centers for Per Cent Moisture													
	32	34	36	38	40	42	44	46	48	50	52	54	56	58
R53 x W23														
R53				1	3	12	20	22	28	21	10	8	4	
B ₁ to] R53]		2	9	29	51	68	42	22	9	7	1	2	2	1
F ₁			2	9	26	32	27	14	12	8	2		1	1
F ₂		1	8	15	28	41	44	41	35	20	23	5	10	4
B ₁ to] W23]	2	3	3	9	21	45	67	47	28	14	11	10	7	3
W23			1	2	1	2	1	5	4	6	5	7	9	11
A158 x Oh40B														
A158					2	6	10	20	26	20	17	6	5	2
B ₁ to] A158]		1		2	12	23	39	58	59	20	20	11	6	4
F ₁					3	4	18	32	32	12	10	9	4	
F ₂			1		5	7	39	36	46	38	31	17	15	11
B ₁ to] Oh40B]					1	4	4	17	39	39	58	38	24	23
Oh40B										2	4	6	10	13
A158 x W23														
A158					1	2	13	26	24	20	12	10	3	3
B ₁ to] A158]		2	4	11	24	47	63	58	30	15	8	2	3	1
F ₁				1	10	32	27	21	13	8	3	3	1	
F ₂	1	4	7	7	21	33	57	39	34	22	14	8	4	3
B ₁ to] W23]				4	3	20	24	44	51	29	31	24	11	5
W23				4	1	2	2	5	6	12	8	10	8	8

TABLE 8 (Continued)

Class Centers for Per Cent Moisture														Total
62	64	66	68	70	72	74	76	78	80	82	84	86	88	
R53 x W23														
3														132
														245
2														136
1	2	1	3	1	1									285
2	3			1	1					1				278
6	10	10	7	6	7	6	9	2	5	1	4			132
A158 x Oh40B														
1														121
5	1													266
1	1													126
4	2													257
10	2	11	3	1				1						287
15	9	9	7	5	6	2	1		1					106
A158 x W23														
1	1	1												118
														268
														120
2	1		1											258
6	4	2	2				1							266
10	5	10	9	5	2	4	3	2		1				124

TABLE 9

SUMMARY OF DOMINANCE RELATIONSHIPS FOR MOISTURE
CONTENT OF EARS HARVESTED AT A UNIFORM
PERIOD FROM PLANTING FOR CORN CROSSES

MS206 x W10

Complete phenotypic
dominance
Partial genic dominance
No epistasis

R53 x W23

Definite heterosis
Complete genic dominance
Possible epistasis

MS206 x Oh40B

Complete phenotypic
dominance
Partial genic dominance
No epistasis

A158 x Oh40B

Slight heterosis
Partial genic dominance
Possible epistasis

R53 x Oh40B

Definite heterosis
Complete genic dominance
Possible epistasis

A158 x W23

Definite heterosis
Complete genic dominance
Possible epistasis

for ear moisture content were generally similar to that for silking date. However, the genic dominance for earliness was not as great.

In the cross (MS206 X Oh40B), complete phenotypic dominance was indicated for a lower moisture percentage since the F_1 mean was not significantly different from that of the early parent. The estimated genetic variance of the backcross to MS206 was much less than that of the F_2 and the backcross to Oh40B so that partial genic dominance was indicated for a lower percentage of ear moisture. Epistasis of dominant genes was probably not involved in this cross because the means of the F_2 and B_1 to Oh40B deviated more from the F_1 mean than would have been expected if epistasis were involved. Dominance relationships for ear moisture content for this cross were very similar to that for silking date. However, somewhat less genic dominance was indicated.

Slight heterosis for a lower moisture content at harvest was exhibited in the cross (R53 X Oh40B) because the means of the F_1 , B_1 to R53, and F_2 generations were significantly less than that of R53. Although significantly different, the F_2 mean was a very close approximation of the F_1 mean. If a high degree of heterosis were involved, the F_2 mean would not be expected to

fall so close to that of the F_1 . Complete genic dominance was indicated in that the estimated genetic variance of the backcross to R53 was negative and was much smaller than that of the F_2 and B_1 to Oh40B populations. The relatively small differences between the means of the F_1 , F_2 , and B_1 to Oh40B populations suggested some degree of epistasis of dominant genes for lower ear moisture content. Epistasis was also indicated for early silking date in this cross (R53 X Oh40B).

In the cross (R53 X W23), definite heterosis for a lower moisture content was exhibited. The means of the F_1 , B_1 to R53, F_2 , and B_1 to W23 were significantly less than that of R53. The backcross to the late inbred W23 had a slightly lower percentage of moisture at harvest than the F_2 and segregated for earliness beyond any of the populations of the cross. It will be shown below that the late silking inbred W23 must have contained dominant genes for a rapid depletion of moisture from the ear. The obtained mean moisture percentage of W23 was rather high, since a considerable number of the ears were harvested before they were very much developed (due to late silking dates). Extreme variability in moisture percentage was noted in the case of the W23 inbred --probably because of more rapid loss of moisture from the ears

of plants that silked earliest. The negative genetic variance calculated for the backcross to R53 indicated that there was complete genic dominance for the genes contributed by R53 for a lower moisture content. However, some of the dominant genes for a lower percentage of moisture must have been contributed by the inbred W23. The relatively small differences between the means of the F_1 , F_2 , and B_1 to W23 indicated that some degree of epistasis of dominant genes may have occurred. The general behavior of the cross (R53 X W23) in dominance relations was similar to that for silking date. However, definite heterosis was exhibited in the ear moisture study. An ear harvest later in the season would have shown more fully the effect of the dominant genes of W23 for rapid ear moisture depletion.

Slight heterosis for a lower moisture content was exhibited in the cross (A158 X Oh40B) because the means of the F_1 and B_1 to A158 were significantly less than the mean of the early inbred A158. Partial genic dominance of genes contributed by A158 for a lower percentage of moisture was indicated in that the genetic variance estimated for the backcross to A158 was less than that of the F_2 and the backcross to Oh40B. Slight epistasis was indicated by the small difference between the F_2 and F_1 mean. However, the

relatively large difference between the F_1 and B_1 to Oh40B means suggested that no epistasis was probably involved. The relative behavior of the populations of the cross (A158 X Oh40B) in the studies of silking date and ear moisture content was quite similar. However, genic dominance appeared not to be as complete in the moisture study.

In the cross (A158 X W23), the mean of the F_1 was significantly less than that of the early parent A158. Thus definite heterosis was exhibited for a lower ear moisture content. Extreme variability was again noted for the inbred W23. Even though the mean of W23 was considerably higher than that of the early parent A158, some of the ears were lower in moisture content (Table 8). The low genetic variance estimated for the backcross to A158, compared with that for the F_2 and backcross to W23, indicated complete genic dominance of genes for a lower ear moisture content contributed by the early parent. However, W23 undoubtedly supplied some dominant genes for rapid depletion of ear moisture --as indicated by the lower values for the means of the F_2 and backcross to the late parent of the cross (A158 X W23), compared to the corresponding means in the cross (A158 X Oh40B). Some degree of epistasis of dominant genes may have been involved in

the cross (A158 X W23). since there was not a significant difference between the F_1 and F_2 means. However, the difference between the means of the B_1 to W23 and the F_1 was considerably larger than would have been expected if epistasis were involved.

In the studies on ear moisture content at a uniform harvest period, heterosis was exhibited in the crosses involving the two inbreds R53 and A158, while MS206 showed complete phenotypic dominance in both crosses. It seemed that the late silking inbred W23 contributed dominant genes for rapid depletion of moisture from the ear because some ears of the inbred were as low in moisture content at harvest as those of the early silking inbreds A158 and R53 (Table 8). The full effect of the dominant genes of W23 was not realized because harvest was made considerably before complete ear development. As in the data on days-to-silking, the mean of the backcross to the early parent in each cross was somewhat earlier than that of the F_1 or early parent. Thus, it appeared that considerable intra-allelic and interallelic gene interactions must have occurred to produce this result

Nature of gene action. Obtained and calculated means based

on the assumption of arithmetic and geometric gene action for the F_2 and backcross populations of each cross are presented in Table 10.

TABLE 10

OBTAINED AND CALCULATED ARITHMETIC AND GEOMETRIC
MEANS FOR MOISTURE CONTENT OF EARS HARVESTED
AT A UNIFORM PERIOD FROM PLANTING

Cross	F ₂ Population		
	Obtained Mean (%)	Calculated Mean	
		Arith- metic (%)	Geo- metric (%)
MS206 x W10	47.1	51.0	49.4
MS206 x Oh40B	44.2	46.8	46.2
R53 x Oh40B	46.2	49.7	49.2
R53 x W23	46.0	49.4	48.9
A158 x Oh40B	49.2	51.7	51.3
A158 x W23	45.5	49.3	49.0
Mean	46.4	49.7	49.0
F value		179.7**	122.4**

* Significant at the 5% level.

** Significant at the 1% level.

TABLE 10 (Continued)

B_1 to P_1 Population			B_1 to P_2 Population		
Obtained Mean (%)	Calculated Mean		Obtained Mean (%)	Calculated Mean	
	Arith- metic (%)	Geo- metric (%)		Arith- metic (%)	Geo- metric (%)
41.1	43.0	43.0	53.8	59.0	56.6
40.4	42.2	42.2	50.2	51.5	50.7
43.0	46.4	46.3	48.3	53.0	52.3
42.2	45.9	45.8	45.6	53.0	52.2
47.4	48.5	48.5	53.2	54.9	54.4
44.4	47.0	46.9	49.4	51.6	51.1
43.1	45.5	45.5	50.1	53.8	52.9
	35.0**	37.4**		14.6*	9.4*

As in the study of silking date, the obtained means in all cases were less than either calculated mean. This appeared to be best explained by the dominance of genes for earliness along with the epistasis which was evident in some crosses. Hardly any differences were obtained for the calculated arithmetic and geometric means for the B_1 to P_1 populations because of the complete phenotypic dominance noted in some crosses and the slight heterosis observed in others. From the analysis of variance, a highly significant difference was found between the mean of the obtained means and that of either the calculated arithmetic or geometric means of the F_2 and B_1 to P_1 populations. In the case of the obtained and calculated means of the B_1 to P_2 populations, the F values indicated a significant difference in both comparisons. However, this did not mean that the fit was poor in the individual crosses. For example, in the crosses (MS206 X Oh40B), (A158 X Oh40B), and (A158 X W23), rather close fits were obtained for the observed and theoretical geometric means. The large differences between the obtained and calculated means of the B_1 to P_2 for the two crosses involving inbred R53 substantiated the hypothesis of epistasis for the dominant genes contributed by R53. From these data it cannot be concluded whether the nature of the gene action affecting

ear moisture content was predominantly arithmetic or geometric. However, the geometric means were slightly closer to the obtained means than the arithmetic means in all cases where the two calculated means differed.

Gene number and heritability. The values calculated for minimum gene number and heritability for moisture content of ears are reported in Table 11. For the crosses (MS206 X W10), (MS206 X Oh40B), and (A158 X Oh40B) the values for gene number were in close agreement with those calculated for silking dates. For the remaining three crosses the calculated gene numbers were much less than those calculated for silking date. It seemed probable that the low gene numbers calculated for the crosses involving W23 may have been due to the fact that at least one of the assumptions of the formula was not valid. This assumption is that one parent supplies only plus factors and the other only minus factors among those in which they differ. As previously indicated, W23 also appeared to contain dominant genes for a lower ear moisture content. Whenever the assumptions of the formula are not true, values are given which may be much smaller than the true gene number.

TABLE 11

ESTIMATED GENE NUMBER AND HERITABILITY VALUES FOR
MOISTURE CONTENT OF EARS HARVESTED AT A
UNIFORM PERIOD FROM PLANTING

Cross	Minimum Gene Number	Maximum Heritability (%)
MS206 x W10	10.5	58
MS206 x Oh40B	5.4	58
R53 x Oh40B	7.1	36
R53 x W23	3.0	54
A158 x Oh40B	4.0	38
A158 x W23	2.3	49
Mean		49

The maximum heritability values reported in Table 11 tended to indicate that good progress could be made from selection within the F_2 generation of any of the crosses on the basis of ear moisture content at the time of harvest indicated. Good progress could also be expected from selection within the backcross populations to the late parent in all crosses, since the genetic variances (Table 7) were large. Only in the case of the crosses (MS206 X W10), (MS206 X Oh40B), and (A158 X Oh40B) could progress be expected from selection within the backcross populations to the early parent because the genetic variance of the other three crosses was negative. In crosses involving W23 heritability values for moisture content were higher than those obtained for silking dates. More progress would be expected from selection for early maturity based on ear moisture content than on silking date in the crosses in which W23 was involved. Similar heritability values for ear moisture content and for silking date were obtained in the cross (A158 X Oh40B). Heritability values for the other five crosses were larger for ear moisture content--indicating that more progress in altering maturity could be expected from selection within segregating populations on the basis of ear moisture content at harvest than from selection on the basis of silking date.

Moisture Content of Ears Harvested Fifty Days From the Date of Silking

In two adjacent replications of the experiment, ears were harvested fifty days after silking, and moisture content of the ear was determined. Pollination was poor for some of the ears of the late-silking inbred W10. In the interpretation of the data, it should be remembered that the ears of plants which silked late had less desirable weather conditions for maturing than ears of plants which silked early. Cooler weather prevailed during the later part of the season than during the earlier portion. Frost occurred before some of the ears were harvested.

According to Shaw and Thom (30), ears harvested fifty days after silking have reached maximum dry weight regardless of variety or weather conditions. In the material harvested before frost, it was apparent on the basis of incomplete denting and high moisture content that all of the ears harvested fifty days after silking had not reached full maturity. Rather and Marston (27) concluded that maximum dry weight was not obtained until the moisture content of ears was reduced to approximately 40 per cent. In the studies of Shaw and Thom, and Rather and Marston, only F_1 double-cross hybrids were used, while the present study

included the F_2 , parental inbred, and backcross populations in addition to the F_1 single-cross hybrid. Even in the F_1 single-cross hybrid there were some ears that apparently were not mature fifty days after silking. The time of maximum ear dry weight was not determined. The means and their standard deviations and the total and genetic variances for ear moisture content fifty days after silking for the crosses are reported in Table 12. Frequency distributions and the total number of ears for the populations of the six crosses are reported in Table 13. The number of plants used in this harvest was much smaller than in the uniform harvest from planting. However, the agreement between the obtained means for the same inbred line involved in different crosses added confidence to the obtained results.

Dominance relationships. Because of the previously mentioned differences in the weather conditions for the maturing of ears, the following discussion of the results is presented with the knowledge that weather conditions may have considerably influenced the results. The populations that were most affected by less favorable weather conditions for maturation of corn were the late parents and the backcrosses to the late parents.

TABLE 12

MEANS AND THEIR STANDARD DEVIATIONS, TOTAL AND GENETIC VARIANCES FOR MOISTURE CONTENT OF EARS HARVESTED FIFTY DAYS AFTER SILKING

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
MS206 x W10				
MS206	45.8	0.47	7.54	
B ₁ to MS206	43.4	0.27	6.50	1.95
F ₁	43.8	0.32	4.55	
F ₂	46.1	0.25	5.80	1.25
B ₁ to W10	49.8	0.38	12.02	7.47
W10	63.4	1.41	49.98	
MS206 x Oh40B				
MS206	44.0	0.39	5.95	
B ₁ to MS206	42.8	0.26	5.04	1.64
F ₁	43.7	0.28	3.40	
F ₂	45.2	0.25	5.32	1.92
B ₁ to Oh40B	48.6	0.40	13.32	9.92
Oh40B	54.3	0.57	11.14	
R53 x Oh40B				
R53	48.5	0.43	7.06	
B ₁ to R53	45.6	0.19	3.04	- 0.34
F ₁	46.2	0.28	3.38	
F ₂	47.1	0.38	12.71	9.33
B ₁ to Oh40B	48.3	0.32	9.33	5.95
Oh40B	54.8	0.68	15.31	

TABLE 12 (Continued)

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
R53 x W23				
R53	47.3	0.29	3.19	
B ₁ to R53	44.0	0.20	3.32	0.32
F ₁	43.1	0.26	3.00	
F ₂	43.8	0.29	8.09	5.09
B ₁ to W23	44.3	0.25	5.06	2.06
W23	46.6	0.98	35.40	
A158 x Oh40B				
A158	49.3	0.45	7.20	
B ₁ to A158	47.5	0.35	10.67	4.70
F ₁	48.1	0.40	5.97	
F ₂	49.2	0.34	9.15	3.18
B ₁ to Oh40B	50.6	0.32	9.20	3.23
Oh40B	55.8	0.62	12.71	
A158 x W23				
A158	47.6	0.46	8.75	
B ₁ to A158	45.4	0.21	3.74	1.28
F ₁	45.4	0.26	2.46	
F ₂	46.1	0.42	14.51	12.05
B ₁ to W23	47.2	0.38	12.42	9.96
W23	49.6	1.40	59.15	

TABLE 13

FREQUENCY DISTRIBUTION FOR MOISTURE CONTENT OF EARS HARVESTED FIFTY DAYS FROM THE DATE OF SILKING FOR POPULATIONS OF CORN CROSSES

Population	Per Cent Moisture																			
	33	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
MS206 x W10																				
MS206					1	1	2	4	5	5	5	4	2	1	1	2	1			
B ₁ to]																				
MS206]		1	6	4	13	15	12	12	11	6	3	5	1							
F ₁			1	3	5	8	8	6	8	2	1	2	1							
F ₂					4	5	10	12	9	21	13	7	8	1	4					
B ₁ to]																				
W10]						1	1	3	3	7	9	12	11	9	9	5	3	3	6	
W10																	2	1	2	
MS206 x Oh40B																				
MS206					3	4	4	7	9	4	3	2	2			1				
B ₁ to]																				
MS206]	1	2	3	10	8	15	10	10	12	3		1		1						
F ₁			1	2	3	7	7	7	11	2	2									
F ₂			1	3	9	12	16	20	6	7	4	6	2	1						
B ₁ to]																				
Oh40B]					2	5	3	5	10	10	15	12	8	3	5			3	1	
Oh40B											2		4	1	3	8	4	4		
R53 x Oh40B																				
R53									4	6	6	7	8	3	2					1
B ₁ to]																				
R53]					3	7	23	16	23	6	5	2	2	1						
F ₁						3	5	8	17	6		1	1				1			
F ₂					1	4	5	15	8	11	15	9	4	6	5	2	1			
B ₁ to]																				
Oh40B]					2	2	9	7	5	18	12	9	12	5	2	2	4			
Oh40B														2	8	3	3	3	2	

TABLE 13 (Continued)

Popu- lation	Per Cent Moisture																			
	33	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
R53 x W23																				
R53									4	3	8	10	4	4	4	1				
B ₁ to]																				
R53]			1		2	4	16	17	16	14	10	1	1							
F ₁					5	7	8	7	10	4	2	1								
F ₂				4	9	12	12	10	16	15	7	3	2	2		1				
B ₁ to]																				
W23]		1		1		9	11	16	12	14	8	8	2		1					
W23	1	1	4	2		3		2			2	2	5	1	1	4	3	3	2	1
A158 x Oh40B																				
A158										3	5	3	8	2	3	3	5	2	1	1
B ₁ to]																				
A158]			1			1	4	8	13	15	13	11	3	9	5	3	1			
F ₁								3	3	9	5	5	4	3	3	1	2			
F ₂							4	6	2	6	3	14	13	7	14	3	5	1		
B ₁ to]																				
Oh40B]								4	4	8	12	9	13	11	13	7	2	2		
Oh40B															1	3	3	4	4	3
A158 x W23																				
A158									2	5	7	6	7	1	5	2	2	2		1
B ₁ to]																				
A158]			1		3	2	13	12	24	12	10	5	3		1					
F ₁					1	1	2	10	10	6	4	3								
F ₂			1		1	5	7	5	10	16	13	7	4	6	4			3		
B ₁ to]																				
W23]					1	4	4	12	15	10	10	9	5	3	5	1	2	2		
W23		1	1	1	1	3	1	1	1	2		3	4		1	2	2			

A summary of the dominance relationships for the moisture content of ears harvested fifty days after silking is presented in Table 14. For the cross (MS206 X W10), slight heterosis was exhibited for a lower ear moisture content fifty days after silking as evidenced by a comparison of the mean of the F_1 with the early parent MS206 (Table 12). Since the genetic variance of the backcross to MS206 was much less than that of the backcross to W10, it appeared that there was a rather high degree of genic dominance for lower ear moisture content for genes contributed by MS206. Since the genetic variance estimated for the F_2 was slightly less than that of the B_1 to MS206 population, it was believed that no genic dominance was actually involved in this cross. Epistasis did not appear to be involved because of the relatively large differences between the means of the F_1 , F_2 , and B_1 to W10. Inbred W10 was extremely high and variable in moisture. This condition was probably due to extreme lateness in silking, differences in ear pollination, and varying weather conditions for ear-drying associated with differences in silking. The frequency distribution on silking date (Table 3) shows that the ears of W10 had from thirty to fifty-one days after silking to develop before killing frost occurred on September 29.

TABLE 14

SUMMARY OF DOMINANCE RELATIONSHIPS FOR MOISTURE
CONTENT OF EARS HARVESTED FIFTY DAYS AFTER
SILKING FOR CORN CROSSES

MS206 x W10

Slight heterosis
No genic dominance
No epistasis

R53 x W23

Definite heterosis
Partial genic dominance
Possible epistasis

MS206 x Oh40B

Complete phenotypic
dominance
Partial genic dominance
No epistasis

A158 x Oh40B

Slight heterosis
(Evidence for or against
genic dominance not clear)
Possible epistasis

R53 x Oh40B

Slight heterosis
Complete genic dominance
Possible epistasis

A158 x W23

Slight heterosis
Almost complete genic
dominance
Possible epistasis

In the cross (MS206 X Oh40B), the mean of the F_1 and B_1 to MS206 were close approximations of the mean of MS206. Complete phenotypic dominance was indicated for a lower ear moisture content. The genetic variance of the backcross to MS206 was slightly smaller than that of the F_2 and much smaller than the genetic variance estimated for the backcross to Oh40B. Although part of the variability for the B_1 to Oh40B can probably be explained by more variation in weather conditions for ear-drying, it is believed that there was slight genic dominance for lower ear moisture for the genes contributed by MS206. Because of the relatively large difference between the mean of the F_1 and B_1 to Oh40B, epistasis appeared not to be involved in this cross. Segregation in the backcross to MS206 for lower ear moisture (Table 13) beyond that of the F_1 or MS206 indicated that considerable intra-allelic and interallelic gene interactions must have occurred. Results for ear moisture content fifty days after silking for the cross (MS206 X Oh40B) were similar to results obtained for silking date and ear moisture content at a uniform period from date of planting.

Slight heterosis was exhibited for a lower moisture content in the cross (R53 X Oh40B), since the F_1 mean was significantly

less than that of R53. Because the means of the first five populations were relatively close together and very little segregation for high ear moisture beyond the F_1 was observed in the F_2 and B_1 to Oh40B populations of the frequency distribution, it appeared that epistasis was involved in this cross. Also, in the studies of silking date and of ear moisture content at a uniform harvest period from planting, some degree of epistasis for earliness was exhibited in the crosses involving R53. The negative genetic variability of the backcross to R53 suggested complete genic dominance of genes for a lower ear moisture content fifty days after silking contributed by R53.

A comparison of the F_1 mean of the cross (R53 X W23) with that of the two parents revealed definite heterosis for a lower percentage of moisture fifty days after the date of silking. The means of the two parents were approximately equal. However, W23 was later in silking and the ears had less favorable weather conditions for drying. Because there was not a significant difference between the means of B_1 to R53 and B_1 to W23, it appeared that both parents contributed dominant genes to the observed heterosis. The lower genetic variance of the B_1 to R53 compared to that of the F_2 and B_1 to W23 indicated some degree of genic dominance

for the genes contributed by R53. However, similar segregation for lower ear moisture in both backcross populations (Table 13) indicated intermediate genic dominance. Since both parents apparently contained dominant genes for lower moisture content, the inheritance data could not be expected to be critical on genic dominance. Because of the small differences between the means of the F_1 , F_2 and the backcrosses, some degree of epistasis may have been involved. The extreme variability in ear moisture content of W23 may have been due to the variability in silking date and more rapid loss of moisture in the ears that silked earlier. In this cross, results for moisture content of ears harvested fifty days after silking were different from those harvested at a uniform period from planting. In the uniform ear harvest from planting date, the effects of the W23 genes for rapid ear moisture depletion had not been fully realized and were masked to some extent by dominant genes of R53 for early silking.

In the cross (A158 X Oh40B), slight heterosis was exhibited for a lower percentage of ear moisture for ears harvested fifty days after silking--as indicated by the significant difference between the means of the F_1 and A158. Because the genetic variances of the backcrosses and the F_2 were approximately the same, the

evidence for or against genic dominance was not clear. Slight segregation for lower ear moisture content beyond that of the F_1 and A158 occurred in the backcross to A158 and the F_2 --indicating that intra-allelic and interallelic gene interactions occurred. The closeness of the means of the first five populations indicated that epistasis may have been involved in this cross.

Slight heterosis for lower moisture content was exhibited in the cross (A158 X W23), since the mean of the F_1 was significantly less than that of A158. Complete genic dominance was indicated for the genes contributed by A158 because the genetic variance of backcross to A158 was small and much less than that of the F_2 and backcross to W23. However, W23 most likely contributed some dominant genes for rapid moisture depletion because several ears were lower in moisture content at harvest than A158, and similar segregation for low ear moisture occurred in the backcross populations (Table 13). The large variability of W23 may have been due to less favorable weather conditions for drying of ears on plants that silked late. Some epistasis may have been involved because of the relatively small differences between the means of the F_1 , F_2 , and the backcrosses. The characteristics of the dominance relations obtained in the study of the moisture content of ears

harvested by the two methods were somewhat different. At the harvest of ears at a uniform period from planting, the full effect of the genes for rapid ear moisture depletion contained by W23 had not been fully realized.

A comparison of the dominance relationships for the three maturity studies revealed that some degree of heterosis for earliness was exhibited in the crosses (R53 X Oh40B), (A158 X Oh40B), and (A158 X W23) in every comparison. The cross (MS206 X W10) showed complete phenotypic dominance for earliness in the studies of silking date and ear moisture content at a uniform harvest period from planting. However, slight heterosis was exhibited in the ear harvest fifty days after silking. Complete phenotypic dominance for low moisture was indicated for the cross (MS206 X Oh40B) for both ear moisture studies. However, slight heterosis was exhibited for early silking. In the cross (R53 X W23), complete phenotypic dominance was indicated for early silking and definite heterosis for the two ear moisture studies. The changes of environment during the growing season may have been an important factor in determining whether a particular cross exhibited phenotypic dominance or heterosis for the three maturity studies. In maturity studies of tomatoes, Powers (22) showed that phenotypic

dominance may be exhibited by a cross in one season and that heterosis may be clearly indicated in a different season. This evidence was presented in support of the hypothesis that heterosis and dominance represent degrees of identical phenomena and are dependent upon the same physiological genetic processes.

Complete or almost complete genic dominance for earliness was indicated for the crosses (R53 X Oh40B) and (A158 X W23) in all three maturity studies. For the cross (MS206 X W10), complete genic dominance for earliness was indicated for the studies on silking date and moisture content of ears harvested at a uniform period from planting. However, in the harvest fifty days after silking intermediate genic dominance for ear moisture content was exhibited. Complete genic dominance for earliness was exhibited in the cross (MS206 X Oh40B) for silking date and partial genic dominance for both moisture studies. For the cross (R53 X W23), complete genic dominance for earliness was indicated in the studies of silking date and moisture content of ears harvested at a uniform period from planting. However, for the harvest fifty days after silking, only partial genic dominance was exhibited. Complete genic dominance for earliness was indicated for silking in the cross (A158 X Oh40B). However, partial genic

dominance for lower ear moisture was exhibited for the harvest at a uniform period from planting, and evidence for or against genic dominance was not clear for the harvest fifty days after silking.

In all three maturity studies, no epistasis was evident in the two crosses involving the early inbred MS206. Some degree of epistasis was possibly involved in the remainder of the crosses. However, it was exhibited to a stronger degree in the crosses involving R53.

Nature of gene action. Calculated means based on the assumption of arithmetic or geometric gene action for the F_2 and backcross populations for ear moisture content fifty days after silking are presented in Table 15. In all comparisons the obtained means were less than the calculated means and the differences between the two calculated means were small. The calculated B_1 to P_1 means were identical in almost all cases because of the small differences obtained between the F_1 and P_1 means. The analysis of variance revealed a highly significant difference between the mean of the obtained means and the mean of the calculated arithmetic or geometric means for the F_2 and B_1 to P_1 populations.

For the B_1 to P_2 populations, the calculated arithmetic and geometric means differed very little, and the mean of the obtained

TABLE 15

OBTAINED AND CALCULATED ARITHMETIC AND GEOMETRIC
MEANS FOR MOISTURE CONTENT OF EARS HARVESTED
FIFTY DAYS AFTER SILKING

Cross	F ₂ Population		
	Obtained Mean (%)	Calculated Mean	
		Arith- metic (%)	Geo- metric (%)
MS206 x W10	46.1	49.2	48.6
MS206 x Oh40B	45.2	46.4	46.2
R53 x Oh40B	47.1	48.9	48.8
R53 x W23	43.8	45.0	45.0
A158 x Oh40B	49.2	50.3	50.2
A158 x W23	46.1	47.0	47.0
Mean	46.3	47.8	47.6
F value		21.8**	30.2*

* Significant at the 5% level.

** Significant at the 1% level.

TABLE 15 (Continued)

B ₁ to P ₁ Population			B ₁ to P ₂ Population		
Obtained Mean (%)	Calculated		Obtained Mean (%)	Calculated	
	Arith- metic (%)	Geo- metric (%)		Arith- metic (%)	Geo- metric (%)
43.4	44.8	44.8	49.8	53.6	52.7
42.8	43.9	43.9	48.6	49.0	48.7
45.6	47.4	47.3	48.3	50.5	50.3
44.0	45.2	45.2	44.3	44.9	44.8
47.5	48.7	48.7	50.6	52.0	51.8
45.4	46.5	46.5	47.2	47.5	47.5
44.8	46.1	46.1	48.1	49.6	49.3
	126.8**	164.7**		6.9*	6.8*

means was significantly different from that of either calculated mean. In the crosses (MS206 X Oh40B), (R53 X W23), and (A158 X W23), the fit was very close for the obtained and either calculated mean of the B_1 to P_2 population.

As in the studies on silking date and ear moisture content at a uniform period from planting, it could not be concluded whether the nature of the gene action affecting moisture content of ears harvested fifty days after silking was either arithmetic or geometric. In all cases where the arithmetic and geometric means differed, there was slightly closer agreement between the geometric and obtained means.

Gene number and heritability Values for minimum gene number and heritability for moisture content of ears harvested fifty days after silking are reported in Table 16. The range in gene numbers was great. The unusually high calculated gene number, 54, for (MS206 X W10) was a consequence of a wide difference between the two parents causing a large D^2 value in the numerator of the gene number formula. Further, since the F_2 and the F_1 did not differ greatly in variability, the denominator became small. In the harvest fifty days after silking, gene numbers were relatively

TABLE 16

ESTIMATED GENE NUMBER AND HERITABILITY VALUES FOR
MOISTURE CONTENT OF EARS HARVESTED
FIFTY DAYS AFTER SILKING

Cross	Minimum Gene Number	Maximum Heritability (%)
MS206 x W10	54.3	22
MS206 x Oh40B	10.8	36
R53 x Oh40B	1.3	73
R53 x W23	0.7	63
A158 x Oh40B	3.2	35
A158 x W23	0.3	83
Mean		52

small for all three maturity studies--with the exception of MS206 X W10. Heritability values were high for the crosses (R53 X Oh40B), (R53 X W23), and (A158 X W23), and more progress could be expected from selection within the F_2 populations of these crosses for ears with low moisture content fifty days after the date of silking. As would be expected, the lowest heritability value for the cross (MS206 X W10) was associated with the highest gene number. In the three maturity studies, high heritability values were generally associated with low gene numbers--indicating that more rapid progress from selection could be expected in the crosses with the lower gene numbers.

EXPERIMENTAL RESULTS ON EAR WEIGHT

A study was made of the dry weight of ears of corn harvested from plants of the different populations for the two different harvesting systems. Results on the inheritance of ear weight cannot be considered critical, since many ears were not fully matured at harvest. However, it was believed that the information obtained was of some interest. The ear weights reported actually contain approximately two per cent moisture. Only the main developed ear of each plant was harvested. There were very few plants where the second ear had developed.

Weight of Ears Harvested at a Uniform Period From Date of Planting

Individual ear weights were determined for the six replications of the experiment harvested at a uniform period from the date of planting. Since the date of harvest was approximately fifty days after half of the plants in the entire experiment had silked, ears of plants which silked late had not reached maximum development. The means, their standard deviations, and the total and genetic variances for weight of ears harvested at a uniform

period from the date of planting are reported in Table 17. Frequency distributions and the total ear numbers for the populations of the different crosses are reported in Table 18. Environmental effects were extremely large. Variances of the parents were not used as measures of environmental variance in the estimation of genetic variance because of the relatively low variabilities associated with the small mean values.

Dominance relationships. In all crosses, comparison of the F_1 mean with that of either parent showed that considerable heterosis was exhibited for a larger ear weight. The fact that the F_2 means were much less than those of the F_1 supports the hypothesis of heterosis. In the crosses (MS206 X W10), (MS206 X Oh40B), (A158 X Oh40B), and (A158 X W23), it appeared that both parents were contributing dominant genes for yield almost equally because of the relatively small differences between the means of the backcrosses in each cross. However, it is believed that the means of the backcrosses to the late parents would have been significantly larger than those of the backcrosses to the early parents with equal periods for ear development. Thus, the late parents probably contributed more dominant genes for heterosis than the early parents in these four crosses.

TABLE 17

MEANS AND THEIR STANDARD DEVIATIONS, TOTAL AND
GENETIC VARIANCES FOR WEIGHT OF EARS
HARVESTED AT A UNIFORM PERIOD
FROM PLANTING

Population	Mean Grams	S.D. of Mean	Total Variance	Genetic Variance
MS206 x W10				
MS206	59.0	1.73	306.08	
B ₁ to MS206	127.2	2.04	1139.81	-185.37
F ₁	188.6	3.14	1325.18	
F ₂	125.2	2.05	1202.12	-123.06
B ₁ to W10	129.8	2.50	1606.73	281.55
W10	35.9	1.83	382.52	
MS206 x Oh40B				
MS206	60.5	1.69	317.07	
B ₁ to MS206	132.5	2.45	1451.91	375.82
F ₁	190.7	2.78	1076.09	
F ₂	133.0	2.24	1244.79	168.70
B ₁ to Oh40B	140.5	2.23	1417.15	341.06
Oh40B	84.7	2.94	892.32	
R53 x Oh40B				
R53	78.8	1.34	246.22	
B ₁ to R53	163.8	1.80	898.45	-622.10
F ₁	194.1	3.33	1520.55	
F ₂	136.7	2.07	1172.14	-348.41
B ₁ to Oh40B	144.7	1.92	1063.78	-456.77
Oh40B	81.5	2.81	882.01	

TABLE 17 (Continued)

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
R53 x W23				
R53	79.2	1.28	214.60	
B ₁ to R53	161.1	1.88	865.90	-268.62
F ₁	180.0	2.89	1134.52	
F ₂	129.6	2.12	1276.53	142.01
B ₁ to W23	149.0	1.97	1083.13	- 51.39
W23	71.9	3.03	1212.58	
A158 x Oh40B				
A158	81.3	2.20	586.50	
B ₁ to A158	139.8	2.33	1441.84	-345.28
F ₁	184.0	3.77	1787.12	
F ₂	143.6	2.12	1157.46	-629.66
B ₁ to Oh40B	140.4	2.07	1232.17	-554.95
Oh40B	77.8	2.73	790.14	
A158 x W23				
A158	88.2	2.05	496.53	
B ₁ to A158	140.2	1.83	895.45	-1044.16
F ₁	194.7	4.02	1939.61	
F ₂	139.5	2.25	1310.72	-628.89
B ₁ to W23	144.0	2.44	1583.97	-355.64
W23	77.8	2.64	866.04	

TABLE 18

FREQUENCY DISTRIBUTION FOR WEIGHT OF EARS
HARVESTED AT UNIFORM PERIOD FROM TIME OF
PLANTING FOR POPULATIONS OF CORN CROSSES

Population	Class Centers in Grams for Ear Dry Weight													
	15	25	35	45	55	65	75	85	95	105	115	125	135	145
MS206 x W10														
MS206		4	15	6	22	26	15	12	1	1				
B ₁ to MS206		3	2	4	7	8	4	5	12	18	26	32	36	47
F ₁							3		2	1		3	4	5
F ₂		1		2	10	10	14	10	19	25	25	31	27	36
B ₁ to W10	1	2	2	3	3	9	11	11	13	23	20	25	28	23
W10	26	30	17	15	6	9	8	3						
MS206 x Oh40B														
MS206		4	7	21	18	31	16	8	3	2	1			
B ₁ to MS206		2	1	4	6	6	7	7	10	12	21	26	20	23
F ₁							1	1	1	1	1	3	3	1
F ₂	1	2	4	3		5	3	7	9	12	24	32	37	23
B ₁ to Oh40B	2	4	2	2	2	2	4	7	8	12	23	22	23	37
Oh40B	3	9	3	7	13	10	10	9	16	9	7	4	2	
R53 x Oh40B														
R53				5	17	25	25	27	22	14	2			
B ₁ to R53					1		3	2	4	3	7	17	18	24
F ₁								1	1	2	3	5	4	4
F ₂	1	2	1	2	2	7	8	14	22	18	26	35	25	
B ₁ to Oh40B	1	1	1	1	3	2	7	11	15	13	24	33	33	
Oh40B	9	2	8	12	6	12	14	9	17	11	8	4		

TABLE 18 (Continued)

Population	Class Centers in Grams for Ear Dry Weight													
	15	25	35	45	55	65	75	85	95	105	115	125	135	145
R53 x W23														
R53			2	10	11	16	16	33	27	16	1			
B ₁ to R53		1			2	1	4	2	5	6	9	14	11	14
F ₁						1	2	1			4	6	4	3
F ₂		4	4	6	9	11	10	8	18	16	18	15	22	29
B ₁ to W23	2			3	2	4	2	6	7	17	17	19	20	26
W23	12	10	10	11	8	11	5	18	17	13	6	1	4	3
A158 x Oh40B														
A158		2	2	12	10	7	20	18	18	19	9	3	1	
B ₁ to A158		3	3	2	1	3	9	8	15	11	15	19	28	34
F ₁		1			1	1	1	2	1	4	3	1	6	4
F ₂		1		3	2	3	6	3	10	19	19	17	30	38
B ₁ to Oh40B			2	2	3	6	8	7	11	16	19	26	31	38
Oh40B		5	5	9	14	9	12	14	13	9	10	1	3	1
A158 x W23														
A158	1	1		4	7	8	19	17	19	24	10	6	2	
B ₁ to A158						2	7	9	5	19	15	27	39	42
F ₁					1	1	1	1		4	2	1	4	2
F ₂		1	3	2		2	9	7	10	17	27	25	13	28
B ₁ to W23		1	3	2	8	4	7	9	8	8	8	15	28	19
W23	1	3	10	14	13	7	16	8	18	14	9	6	4	1

For the two crosses involving R53, the means of the backcrosses to R53 were significantly larger than those of the backcrosses to the late parents--supporting the possibility that R53 contributed more dominant genes for yield than either Oh40B or W23. Differences in ear maturity probably would not account for the relatively large difference between the means of the backcrosses to R53 and the means of the backcrosses to the late parents. In Table 19 it can be observed that the means of the B_1 to P_1 populations for the two crosses involving R53 were considerably larger than either calculated mean--supporting the belief in a greater contribution of dominant genes for yield by R53 than by MS206 and A158.

Nature of gene action. The obtained and the calculated means based on the assumption of arithmetic and geometric gene action for weight of ears harvested at a uniform period from planting for the F_2 and two backcross populations of each cross are presented in Table 19. The F values indicated that for the F_2 and B_1 to P_1 populations the mean of the arithmetic means was not significantly different from the mean of the obtained means, while the mean of the geometric means was significantly different from that of the obtained means. The mean of the calculated

TABLE 19

MAINTAINED AND CALCULATED ARITHMETIC AND GEOMETRIC
MEANS FOR WEIGHT OF EARS HARVESTED AT A
UNIFORM PERIOD FROM PLANTING

Cross	F ₂ Population		
	Obtained Mean (gms.)	Calculated Mean	
		Arith- metic (gms.)	Geo- metric (gms.)
06 x W10	125.2	118.0	93.2
06 x Oh40B	133.0	131.7	116.9
x Oh40B	136.7	137.1	124.7
x W23	129.6	127.8	116.6
8 x Oh40B	143.6	131.8	121.0
8 x W23	139.5	138.9	127.0
n	134.6	130.9	116.6
value		3.5	30.7**

* Significant at the 5% level.

** Significant at the 1% level.

TABLE 19 (Continued)

B ₁ to P ₁ Population			B ₁ to P ₂ Population		
Obtained Mean (gms.)	Calculated Mean		Obtained Mean (gms.)	Calculated Mean	
	Arith- metic (gms.)	Geo- metric (gms.)		Arith- metic (gms.)	Geo- metric (gms.)
127.2	123.8	105.5	129.8	112.3	82.3
132.5	125.6	107.4	140.5	137.7	127.1
163.8	136.5	123.7	144.7	137.8	125.8
161.1	129.6	119.4	149.0	126.0	113.8
139.8	132.7	122.3	140.4	130.9	119.7
140.2	141.5	131.0	144.0	136.3	123.1
144.1	131.6	118.2	141.4	130.2	115.3
	5.1	24.5**		13.4*	25.2**

arithmetic means and that of the geometric means for the B_1 to P_2 population were significantly different from the mean of the obtained means. However, the mean of the arithmetic means was closer to agreement with the observed means.

Gene number and heritability. Minimum gene number and maximum heritability values for weight of ears harvested at a uniform period from the time of planting are presented in Table 20. One of the assumptions of the formula--that one parent supplies only plus factors and the other only minus factors among those in which they differ--did not apply in the case of the data on ear weight. The formula gives minimum values when the assumptions do not apply. Since the variance of the F_1 was greater than that of the F_2 for four of the six crosses, gene numbers could not be calculated.

Four of the heritability values reported in Table 20 were negative, since the F_1 variance was greater than that of the F_2 . Low positive values were obtained for the crosses (MS206 X Oh40B) and (R53 X W23). Under the conditions of this harvest, it appears that very little, if any, progress could be expected from selection for high ear weight within F_2 populations, since the environmental variability overshadowed genetic variability.

TABLE 20

ESTIMATED GENE NUMBER AND HERITABILITY VALUES FOR
WEIGHT OF EARS HARVESTED AT A UNIFORM
PERIOD FROM TIME OF PLANTING

Cross	Minimum Gene Number	Maximum Heritability (%)
MS206 x W10	-	-10
MS206 x Oh40B	21.1	14
R53 x Oh40B	-	-30
R53 x W23	19.2	11
A158 x Oh40B	-	-54
A158 x W23	-	-48

Weight of Ears Harvested Fifty Days From the Date of Silking

Ears were harvested from two adjacent replications fifty days after silking, and dry weight determined. The means, their standard deviations, and the total and genetic variances are reported in Table 21. Frequency distributions and total ear numbers for the populations are reported in Table 22. Again it should be remembered that ears harvested toward the later part of the harvesting period were subjected to quite different weather conditions than those harvested earlier. Ears of plants that silked later than eighty-three days after planting did not have a fifty-day period for development after silking because of a killing frost which occurred 133 days after planting.

Dominance relationships. In all crosses, decided heterosis was obtained for heavier ear weight. The means of the F_1 , F_2 , and backcross populations were larger than those of both parents in all crosses. In the crosses (MS206 X W10) and (MS206 X Oh40B), it was apparent that the late parents had contributed more dominant genes to the heterosis for ear weight than the early parent MS206 because the means of the backcrosses to the late parent were significantly larger than those to MS206. It is reasonable to

TABLE 21

MEANS AND THEIR STANDARD DEVIATIONS, TOTAL AND GENETIC VARIANCES FOR WEIGHT OF EARS HARVESTED FIFTY DAYS FROM DATE OF SILKING

Population	Mean Grams	S.D. of Mean	Total Variance	Genetic Variance
MS206 x W10				
MS206	55.9	3.12	331.75	
B ₁ to MS206	126.4	3.41	1034.49	- 1.30
F ₁	179.5	4.80	1035.79	
F ₂	139.4	2.93	806.28	-229.51
B ₁ to W10	151.8	3.85	1259.61	223.82
W10	54.5	4.67	545.63	
MS206 x Oh40B				
MS206	56.8	2.70	285.00	
B ₁ to MS206	122.2	3.51	934.70	353.87
F ₁	187.8	3.72	580.83	
F ₂	127.3	3.65	1160.92	580.09
B ₁ to Oh40B	139.6	3.82	1239.73	658.90
Oh40B	104.1	4.43	668.33	
R53 x Oh40B				
R53	78.9	2.91	322.71	
B ₁ to R53	162.0	2.91	745.27	-372.47
F ₁	195.0	5.16	1117.74	
F ₂	138.6	3.19	893.20	-224.54
B ₁ to Oh40B	143.8	3.18	918.87	-198.87
Oh40B	100.6	5.73	1082.95	

TABLE 21 (Continued)

Population	Mean Days	S.D. of Mean	Total Variance	Genetic Variance
R53 x W23				
R53	87.3	1.68	107.80	
B ₁ to R53	165.8	2.20	396.82	37.40
F ₁	201.5	2.86	359.42	
F ₂	156.5	3.24	989.29	629.87
B ₁ to W23	168.2	3.08	787.46	428.04
W23	104.8	5.31	1044.88	
A158 x Oh40B				
A158	90.6	4.18	629.66	
B ₁ to A158	141.2	3.58	1143.26	318.29
F ₁	194.4	4.66	824.97	
F ₂	143.8	3.42	934.59	109.62
B ₁ to Oh40B	150.8	3.82	1324.66	499.69
Oh40B	92.2	4.99	823.11	
A158 x W23				
A158	95.7	3.81	594.30	
B ₁ to A158	147.6	2.96	753.03	- 36.81
F ₁	205.5	4.62	789.84	
F ₂	148.0	3.85	1247.25	457.41
B ₁ to W23	158.6	4.85	2002.04	1212.20
W23	91.5	6.71	1350.55	

TABLE 22

FREQUENCY DISTRIBUTION FOR WEIGHT OF EARS
HARVESTED FIFTY DAYS FROM TIME OF SILKING
FOR POPULATIONS OF CORN CROSSES

Population	Class Centers in Grams for Ear Weight													
	15	25	35	45	55	65	75	85	95	105	115	125	135	145
MS206 x W10														
MS206			3	4	6	6	9	3	1	2				
B ₁ to MS206			2	1	1	3	2	2	5	6	8	11	8	15
F ₁					1						1			3
F ₂							1	3	3	1	12	13	15	17
B ₁ to W10				1			3	3	3	1	2	6	6	5
W10	1	3	4	2	5	5	1	2	1	1				
MS206 x Oh40B														
MS206			2	7	4	4	12	7	3					
B ₁ to MS206						3	2	3	6	3	6	8	9	8
F ₁														3
F ₂						3	3	3	5	2	6	9	12	8
B ₁ to Oh40B	1	1	1			2			3	6	4	7	10	10
Oh40B			1			1	3	4	4	5	7	2	4	2
R53 x Oh40B														
R53			2	1	2	2	9	10	9	3				
B ₁ to R53								1	1	2	2	1	11	9
F ₁										2		1		
F ₂		1	1		1		1	2	1	3	4	11	17	15
B ₁ to Oh40B			1	1			1		1	6	7	8	7	13
Oh40B			2	1		2	4	3	4	4	2	4	3	2

TABLE 22 (Continued)

Class Centers in Grams for Ear Weight

Total

155 165 175 185 195 205 215 225 235 245 255 265 275

MS206 x W10

34

13 10 2

89

5 3 7 5 8 4 5 2 1

45

8 4 7 6 1 2 1

94

13 11 12 7 6 4 2

85

25

MS206 x Oh40B

39

14 2 4

76

4 2 5 6 8 4 4 5 1

42

10 7 2 1 1 1

87

13 12 7 5 2 1

85

1 34

R53 x Oh40B

38

10 12 15 10 8 1 4 1

88

1 1 5 5 5 8 3 6 1 4

42

7 11 7 5 1

88

17 10 11 4 3 1

91

1 1 33

TABLE 22 (Continued)

Population	Class Centers in Grams for Ear Weight													
	15	25	35	45	55	65	75	85	95	105	115	125	135	145
R53 x W23														
R53						2	6	14	10	6				
B ₁ to R53										2		1	1	8
F ₁														
F ₂				1			1	1		1	4	4	11	17
B ₁ to W23									1		2	7	4	6
W23				2		1	5	4	5	4	6	3	2	1
A158 x Oh40B														
A158			1	3	1	2	2	5	7	6	2	6	1	
B ₁ to A158			1					4	3	8	5	9	13	11
F ₁												1		1
F ₂			1				2	2	2	2	1	11	8	13
B ₁ to Oh40B			1	3			1	1	2	2	1	6	5	15
Oh40B			1	2	1	3	3	6	4	4	2	4	1	1
A158 x W23														
A158				2	1	6	3	2	4	9	8	4	1	
B ₁ to A158									2	7	8	5	10	9
F ₁											1			
F ₂		1			1		1	3	1	3	5	5	9	10
B ₁ to W23			1	2	1	2	1	1	4	2	2	3	3	3
W23		1	3	2	1		1	5	4	5	3	1		2

assume that the means of B_1 to W10 and B_1 to Oh40B would have been even larger if some ears had not been stopped in development by frost before harvest. Poor pollination and incomplete ear development before frost contributed to the low mean of W10.

In the cross (R53 X Oh40B), the mean of the backcross to R53 was significantly higher than that of the backcross to Oh40B-- indicating that there was a larger contribution of dominant genes for larger ear weight from the early inbred R53. The same conclusion was made for the previously reported ear harvest

In the crosses (R53 X W23), (A158 X Oh40B), and (A158 X W23), a study of the backcross means and frequency distributions revealed that the contribution of favorable dominant genes for larger ear weight was almost equal for both parents in each cross. However, the means of the backcrosses to the late parents probably would have been somewhat larger under equal weather conditions for ear development. Thus it is impossible to make any definite conclusions on the relative contributions of the two parents of a cross to heterosis for ear weight in these three crosses.

Nature of gene action. Obtained and calculated means for the F_2 and backcross populations are presented in Table 23. F values reported at the bottom of the table indicated that for the

TABLE 23

OBTAINED AND CALCULATED ARITHMETIC AND GEOMETRIC
MEANS FOR WEIGHT OF EARS HARVESTED FIFTY
DAYS AFTER SILKING

Cross	F ₂ Population		
	Obtained Mean (gms.)	Calculated Mean	
		Arith- metic (gms.)	Geo- metric (gms.)
MS206 x W10	139.4	117.4	99.5
MS206 x Oh40B	127.3	134.1	120.2
R53 x Oh40B	138.6	142.4	131.8
R53 x W23	156.5	148.8	138.8
A158 x Oh40B	143.8	142.9	133.3
A158 x W23	148.0	149.6	138.7
Mean	142.3	139.2	127.1
F value		0.51	8.58*

* Significant at the 5% level.

** Significant at the 1% level

TABLE 23 (Continued)

B ₁ to P ₁ Population			B ₁ to P ₂ Population		
Obtained Mean (gms.)	Calculated Mean		Obtained Mean (gms.)	Calculated Mean	
	Arith- metic (gms.)	Geo- metric (gms.)		Arith- metic (gms.)	Geo- metric (gms.)
126.4	117.7	100.2	151.8	117.0	98.9
122.2	122.3	103.3	139.6	146.0	139.8
162.0	137.0	124.0	143.8	147.8	140.1
165.8	144.4	132.6	168.2	153.2	145.3
141.2	142.5	132.7	150.8	143.3	133.9
147.6	150.6	140.2	158.6	148.5	137.1
144.2	135.8	122.2	152.1	142.6	132.5
	2.89	18.1**		2.44	6.50

F_2 and backcross populations no significant differences existed between the mean of the obtained means and that of the calculated arithmetic means. Significant differences were obtained between the mean of the obtained means and that of the geometric means for the F_2 and B_1 to P_1 populations. The F value obtained for the comparison of the obtained and geometric means of the B_1 to P_2 population approached significance.

For both harvests, the data fit the hypothesis that the effects of the genes determining ear dry weight were predominantly additive. This conclusion was in agreement with that of Neal (20) and Kinman and Sprague (14).

Gene number and heritability Since the F_1 variance was greater than that of the F_2 in the crosses (MS206 X W10) and (R53 X Oh40B), gene numbers could not be calculated. Minimum gene numbers and heritability estimates for crosses for which calculations could be made are given in Table 24. In view of the effects of immaturity at harvest and failure of one of the basic assumptions of the formula to apply, these gene numbers are undoubtedly much lower than the real values.

Relatively high heritability values for the crosses (MS206 X Oh40B) and (R53 X W23) indicated that good progress could be

TABLE 24

ESTIMATED GENE NUMBER AND HERITABILITY VALUES FOR
WEIGHT OF EARS HARVESTED FIFTY DAYS AFTER SILKING

Cross	Minimum Gene Number	Maximum Heritability (%)
MS206 x W10	-	-29
MS206 x Oh40B	5.4	50
R53 x Oh40B	-	-25
R53 x W23	4.4	64
A158 x Oh40B	24.2	12
A158 x W23	6.8	37

expected from selection within the F_2 populations for a larger ear weight fifty days after silking. It should be remembered that the heritability values calculated should be considered as maximum values because the genetic variability used in the calculations most likely contained some variability which was not additive. Only additive genetic variability is considered heritable. In the crosses (MS206 X W10) and R53 X Oh40B), the negative heritability values indicated that no progress could be expected in these crosses from selection for ear weight within a similar F_2 generation. As expected, the lowest positive heritability value was obtained for the cross (A158 X Oh40B), for which a high gene number had been calculated.

Since the crosses (MS206 X Oh40B) and (R53 X W23) gave the highest heritability estimates for both harvests, better progress in selection for ear weight within the segregating generations of these crosses could be expected. Heritability values for ear weight were generally low in most cases; this agrees with the estimates reported by Robinson et al (29) for yield in two corn crosses.

DISCUSSION

Inheritance of corn maturity as measured by silking date and ear moisture content at two different harvests was generally similar in the six crosses studied. Either complete phenotypic dominance or slight heterosis for earliness of silking was exhibited in every cross. Lindstrom (16) and Yang (40) have reported dominance for early silking in maize. Heterosis for early silking of corn hybrids was reported by Yang (40) and Leng (15). Some degree of heterosis for earliness was probably exhibited in all of the crosses in the maturity studies although the mean of the F_1 was not always significantly less than the early parent. In each cross the infrequency of recovery of the extremes in lateness of the late parents indicated that slight heterosis was probably involved. However, it appeared that a large amount of heterosis was not exhibited for earliness because, for each cross, the mean of the backcross to the early parent was earlier than the F_1 mean, and the expected deviation between the F_1 and F_2 means did not occur. Therefore, the major portion of the observed earliness of the F_1 in each cross must have been caused by dominance of genes for earliness.

The phenotypic dominance for earliness leads to the conclusion that crosses of early X late inbred lines of corn may be successfully used in double-cross hybrids where the objective is to maintain the earliness of the early lines and the yielding ability of the later maturing lines.

Complete genic dominance for early silking was exhibited in each cross, and either partial or complete genic dominance was indicated for a lower ear moisture content at a uniform harvest period from planting. Thus, intra-allelic gene interactions were of importance in effecting the complete phenotypic dominance indicated in some crosses and the slight heterosis exhibited in others. In the ear harvest fifty days after silking, variations from none to complete genic dominance for low ear moisture were indicated. The greater degree of genic dominance exhibited for early silking in all crosses, as compared to the slight or no genic dominance for low ear moisture fifty days after silking, suggests that dominant genes for early silking are not effective for rapid ear moisture depletion. Or there may even be two groups of genes--one effecting early silking, and another group effecting low ear moisture. Some inbreds--such as W23--may be late in silking, but contain dominant genes for rapid drying of

ears. Consequently, classification of inbred lines based only on silking date may not furnish the desired information on maturation.

Epistasis of dominant genes for earliness was not evident in any of the maturity studies for the two crosses involving MS206. However, some degree of epistasis may have been involved in the rest of the crosses. Dominant genes of R53 appeared to exhibit epistasis strongly. In a breeding program, it appears that practical use may be made of early inbred lines that contain dominant epistatic genes for early maturity. Where early and late inbreds are included in the production of a double-cross hybrid or a synthetic variety, greater uniformity in maturity may be expected by the use of early inbreds that contain dominant epistatic genes.

Theoretically, double crosses of the type $(E_1 \times E_2) \times (L_1 \times L_2)$ should be less variable in maturity than crosses of the type $(E_1 \times L_1) \times (E_2 \times L_2)$. Eckhart and Bryan (6) reported this to be true in studies of silking date and suggested that it would be true for ear moisture. In studies of silking date and ear moisture, Pinnell (21) found that one double cross of the type $(E_1 \times L_1) \times (E_2 \times L_2)$ was less variable, and another was more

variable, than the type $(E_1 \times E_2) \times (L_1 \times L_2)$. Thayer (34) concluded that double crosses of the type $(E_1 \times L_1) \times (E_2 \times L_2)$ were no more variable in ear moisture content than those of the type $(E_1 \times E_2) \times (L_1 \times L_2)$. If the dominant genes in the early inbreds exhibit epistasis, it is apparent that the double cross of the type $(E_1 \times L_1) \times (E_2 \times L_2)$ may be no more variable than the type $(E_1 \times E_2) \times (L_1 \times L_2)$ or a combination of four lines that are similar in maturity. This appears to be a possible explanation for the differences in the results reported on variability in maturity for double crosses of the type $(E_1 \times L_1) \times (E_2 \times L_2)$.

The mean of the backcross to the early parent in each cross was earlier in silking date or lower in ear moisture content than the F_1 or the early parent. It is probable that intrallelic and interallelic gene interactions along with some degree of heterosis were mainly responsible for this relationship.

In the majority of the maturity studies, the variability of the backcross to the early parent of each cross was relatively small and no more variable than the F_1 . Because of the uniformity and the earliness of the backcrosses to the early parent, it appears that some practical use may possibly be made of them in the production of hybrids possessing high yielding ability,

earliness and uniformity of maturity, and other desirable characteristics. Especially would this apply to regions--such as Michigan--with relatively short growing seasons. Early inbred lines could be combined with extremely late inbreds which have demonstrated exceptional combining ability for yield in the following scheme:

$$[(E_1 \times L_1) E_1 \times (E_2 \times L_2) E_2],$$

where E_1 and E_2 are early lines containing dominant and epistatic genes--such as R53 and A158, and L_1 and L_2 are extremely late lines--such as 38-11 and L317 which are used in the production of the extensively used double-cross hybrid U. S. 13. The proposed method should result in a hybrid exhibiting more earliness and uniformity of maturity, than would be obtained with the conventional method of combining early and late lines $(E_1 \times L_1) \times (E_2 \times L_2)$. The uniformity in earliness of the double-cross hybrid $(E_1 \times E_2) (L_1 \times L_2)$ would be equaled by the use of the suggested method. A hybrid of the proposed type might be slightly lower in yielding ability than the $(E_1 \times L_1) (E_2 \times L_2)$ type because of a lower frequency of genes of the late inbreds, which possess outstanding combining ability for yield.

Hybrid seed production by the proposed method would be much less difficult and expensive than by the conventional method. For the production of equal quantities of double-cross seed, the proposed method would require a smaller amount of seed of the inbreds and a much smaller quantity of single-cross seed ($E \times L$) than that required for the method $(E_1 \times L_1) \times (E_2 \times L_2)$. The smaller amount of single-cross seed required for the suggested method is especially important because of the difficulty of matching early and late inbreds for seed production. In the suggested method the backcrosses to the early parents would be made by detasseling the F_1 and using the early inbred as the pollen parent. Therefore, a much greater yield of foundation backcross seed per acre would be obtained for combining the two backcrosses than would be obtained by producing foundation single-cross seed for making the conventional double cross. The backcross seed would be produced on vigorous F_1 plants while the seed for the making of the normal double cross is produced on inbred plants.

It could not be concluded whether the nature of the gene action for silking date and moisture content was predominantly arithmetic or geometric. However, in all cases where the two

calculated means differed, the theoretical geometric means were closer to agreement with those obtained.

Gene numbers calculated for the crosses ranged from 5 to 19 for silking date, 2 to 11 for moisture content of ears harvested at a uniform period from planting, and 1 to 54 for moisture content of ears harvested fifty days after silking. All of the assumptions of Wright's formula did not always apply to the data in these studies. However, it is believed that the values obtained may be of some value in indicating the relative progress that may be expected from selection for early silking date or low ear moisture in the segregating populations of the crosses. More rapid progress would be expected for the crosses where lower gene numbers were involved.

For the four crosses involving R53 and A158, the much lower gene numbers obtained for the moisture content of ears harvested fifty days after silking than for silking date may indicate that some or all of the dominant genes affecting silking date were not active for ear moisture depletion.

Heritability values must be considered as a maximum because genetic variability other than that which is strictly additive was included. Higher average heritability values were obtained for

ear moisture content at both harvests than for silking date--indicating that more progress could be expected from selection on the basis of ear moisture content than on the basis of silking date. From a practical standpoint, selection for ear maturity should normally be done at a much later uniform harvest date than the one reported in this investigation; it probably would not be done fifty days after silking of individual plants.

The immaturity of ears at both harvest periods may have influenced the accuracy of the conclusions reached on ear weight or yield. A high degree of heterosis was exhibited for heavier ear dry weight in all crosses in both harvests. Although the late inbreds W10, Oh40B, and W23 contributed much to the observed heterosis, the early inbred R53 was noteworthy in its contribution. Thus R53 should be a good early inbred for use in the development of high-yielding and early hybrids.

The conclusion that the genes affecting ear weight followed the arithmetic scale was in agreement with the results of Neal (20) and Kinman and Sprague (14). Predicting yields of double crosses from single-cross yields is based on the assumption of arithmetic gene action.

Gene numbers that could be calculated for ear weight were probably much too low because at least one of the basic assumptions of the formula--that one parent supplies only plus factors and the other, only minus factors--was obviously not true. Both parents contributed to the observed heterosis.

The low heritability values for the ear harvest at a uniform period from planting indicated that very little, if any, progress could be expected from selection for heavier ear weight within the segregating progenies of any of the crosses studied. However, for the ear harvest fifty days after silking, rather good heritability values were calculated for the crosses (MS206 X Oh40B), (R53 X W23), and (A158 X W23).

For ear weight and ear moisture content at both harvests, higher heritabilities were obtained for the crosses (R53 X W23), (MS206 X Oh40B), and (A158 X W23).

SUMMARY

The inheritance of maturity and ear weight were investigated with six different crosses of early X late inbred lines of corn. Dominance relationships, gene numbers, nature of gene action, and heritability were studied. Silking date, moisture content of ears harvested at a uniform period from time of planting, and ear moisture content fifty days after silking were used as measures of maturity. Data on ear weight were obtained at two harvest periods.

1. In each cross, either complete phenotypic dominance or slight heterosis for earliness was indicated in all maturity studies. Some degree of heterosis for earliness was probably involved in each cross. However, the major portion of the observed earliness appeared to be due to dominance of genes.

2. Complete genic dominance for early silking, partial to complete genic dominance for lower ear moisture at a uniform harvest period from planting, and variations from none to complete genic dominance for lower ear moisture fifty days after silking were indicated for the crosses. The data suggest that the classification of inbred lines entirely on the basis of silking date may

not furnish the desired information on maturation. Some inbreds contained dominant genes for early silking that did not appear to effect ear moisture depletion. Other inbreds were late in silking but contained dominant genes for rapid ear drying.

3. Epistasis for earliness appeared to be exhibited by the dominant genes contributed by the early inbred R53 and possibly by A158. Early inbreds containing dominant epistatic genes for early maturity should provide more uniformity of maturity in a double cross of the type $(E_1 \times L_1) \times (E_2 \times L_2)$ than an early inbred with dominant but nonepistatic genes for earliness. Epistasis of dominant genes may aid in explaining reports that crosses of the type $(E_1 \times L_2) \times (E_2 \times L_2)$ were no more variable than that of the type $(E_1 \times E_2) \times (L_1 \times L_2)$.

4. In the maturity studies, it could not be concluded whether gene action was following either the arithmetic or the geometric schemes. In all cases where calculated means differed from the actual means, the geometric means were closer to agreement with the obtained. It was probable that both types of gene action were involved.

5. Minimum gene numbers ranged from 5 to 19 for silking data, from 2 to 11 for moisture content of ears harvested at a

uniform period from planting, and from 1 to 54 for moisture content of ears harvested fifty days after silking.

6. Maximum heritability values ranged from 11 per cent to 48 per cent for silking date, 36 per cent to 58 per cent for moisture content of ears harvested at a uniform period from planting, and 22 per cent to 83 per cent for moisture content of ears harvested fifty days after silking. Heritabilities for ear moisture content averaged higher than heritability of silking date. There was an indication that silking date was affected more by environment than ear moisture content.

7. Considerable heterosis was exhibited for heavier ear weight in all crosses. Of the early inbreds, R53 was exceptional in its contribution of favorable genes for heavier ear weight. Genes affecting ear weight followed the arithmetic scheme.

8. Maximum heritability values calculated for ear weight indicated that very little, if any, progress could be expected from selection for heavy ears within the segregating progenies of any of the crosses at the uniform harvest period. However, good progress could be expected from selection within the F_2 generation of the crosses (MS206 X Oh40B), (R53 X W23), and (A158 X W23) in the case of a harvest fifty days after silking.

9. It was proposed that an F_1 combination of early lines containing dominant epistatic genes with late lines possessing exceptional combining ability for yield may be made as follows:

$$[(E_1 \times L_1) E_1] \times [(E_2 \times L_2) E_2].$$

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CORRELATION COEFFICIENTS BETWEEN EAR WEIGHT AND MATURITY

Correlation coefficients were calculated between ear dry weight and ear moisture percentage and between ear dry weight and number of days from planting to silking for both harvesting systems. Standard procedure was used (31). Although correlation coefficients measure the relationship between the expression of two characteristics in a segregating generation of a cross, they do not indicate how much of the measured relationship is heritable. To eliminate some of the nonheritable effects, genetic correlations were calculated for the crosses. The formula supplied to Burton (2) by Comstock was used:

$$\text{Genetic correlation} = \frac{cvXYF_2 - cvXYF_1}{\sqrt{(vXF_2 - vXF_1)(vYF_2 - vYF_1)}}$$

where cv = covariance and v = variance.

Correlation coefficients between ear weight and ear moisture percentage and between ear weight and days from planting to silking for both harvest periods are shown in Table 25. Significant negative correlations were obtained in almost all cases, indicating that heavy ear weight was associated with early silking and with

low ear moisture content. No difficulty should be encountered in the selection of heavy ears low in moisture percentage within any of the populations of the crosses.

In general, slightly higher negative correlations were obtained for the ear harvest at a uniform period from planting than for the harvest fifty days after silking. The larger number of immature ears at the uniform ear harvest may have been largely responsible for the higher values for this harvest period.

Genetic correlations for the crosses are shown in Table 26. Values for some crosses could not be calculated because the variability in ear weight of the F_1 was greater than that of the F_2 . In general, genetic correlations were similar, indicating that plants which silked early in most cases produced heavy ears and heavy ears were relatively low in moisture percentage at the harvest periods. In a breeding program for the selection of plants with high yielding ability and early maturity it would be possible to select heavy ears with low moisture content.

TABLE 25

CORRELATION COEFFICIENTS BETWEEN EAR WEIGHT
AND MATURITY IN CORN CROSSES

Population	Ear Harvest at Uniform Period From Planting		Ear Harvest Fifty Days After Silking	
	XY ¹	XZ	XY	XZ
MS206 x W10				
B ₁ to MS206	-0.5**	-0.4**	-0.4**	-0.3**
F ₁	-0.8**	-0.9**	-0.5**	-0.8**
F ₂	-0.6**	-0.7**	-0.4**	-0.5**
B ₁ to W10	-0.8**	-0.6**	-0.6**	-0.7**
R53 x Oh40B				
B ₁ to R53	-0.4**	-0.9**	-0.3**	-0.5**
F ₁	-0.6**	-0.8**	-0.5**	-0.8**
F ₂	-0.4**	-0.5**	-0.6**	-0.5**
B ₁ to Oh40B	-0.7**	-0.7**	-0.6**	-0.7**
A158 x Oh40B				
B ₁ to A158	-0.6**	-0.5**	-0.6**	-0.3**
F ₁	-0.7**	-0.7**	-0.6**	-0.6**
F ₂	-0.5**	-0.5**	-0.5**	-0.4**
B ₁ to Oh40B	-0.7**	-0.7**	-0.7**	-0.7**

TABLE 25 (Continued)

Population	Ear Harvest at Uniform Period From Planting		Ear Harvest Fifty Days After Silking	
	XY	XZ	XY	XZ
MS206 x Oh40B				
B ₁ to MS206	-0.6**	-0.5**	-0.2	-0.2
F ₁	-0.6**	-0.7**	+0.1	-0.4**
F ₂	-0.5**	-0.1**	-0.4**	-0.4**
B ₁ to Oh40B	-0.8**	-0.7**	-0.8**	-0.8**
R53 x W23				
B ₁ to R53	-0.4**	-0.6**	+0.1	-0.1
F ₁	-0.6**	-0.7**	-0.3*	-0.5**
F ₂	-0.6**	-0.7**	-0.3**	-0.3**
B ₁ to W23	-0.5**	-0.7**	-0.2	-0.5**
A158 x W23				
B ₁ to A158	-0.3**	-0.4**	-0.4**	-0.2*
F ₁	-0.8**	-0.9**	-0.4**	-0.8**
F ₂	-0.3**	-0.4**	-0.5**	-0.4**
B ₁ to W23	-0.5**	-0.3**	-0.5**	-0.6**

¹ X = ear dry weight; Y = ear moisture percentage; Z = number of days from planting to silking.

* Significant at the 5% level.

** Significant at the 1% level.

GENETIC CORRELATIONS BETWEEN EAR WEIGHT AND MATURITY IN CORN CROSSES

Cross	Ear Harvest at Uniform Period From Planting		Ear Harvest Fifty Days After Silking	
	XY*	XZ	XY	XZ
MS20 x W10				
MS20 x Oh40B	-0.4	+0.5	-0.9	-0.5
R53 x Oh40B				
R53 x W23	-0.8	-0.9	-0.3	0
A158 x Oh40B			0	+0.2
A158 x W23			-0.7	+0.2

* X = early dry weight; Y = ear moisture content; Z = number of days from planting to silking.