

INHERITANCE OF PROLIFICACY AND MATURITY
IN
CROSSES OF SOUTHERN x NORTHERN MAIZE GERM PLASM

By
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AN ABSTRACT

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Approved E. C. Rossmann

ABSTRACT

Four northern and three southern inbred lines of maize were used to study the inheritance of ear number and days to silking.

Individual plant data were used to obtain estimates of generation means and variances. Gene numbers, dominance relationships and heritability values were calculated.

Gene numbers ranged from one to three for ear number. Dominance relationships varied from complete dominance for genes controlling the two-eared characteristic through no dominance to complete dominance for one ear.

At several locations previous research with germ plasm adapted to the area had indicated that the two-eared characteristic was recessive in nature. This study indicated that the dominance relationships varied with the particular parents used. No generalized statement regarding the dominance of the one-eared condition is valid as shown by the lack of dominance in the cross W64A x T115 which represented the least and the most prolific inbreds used in this study.

Epistatic effects varied from no epistasis to epistasis for one ear. Heritability values varied from 0.0 to 1.0, averaging 0.439. Previously reported heritability values for

ear number have been somewhat lower, perhaps due to the use of populations less genetically diverse.

The expression of ear number was not significantly affected by the competition or lack of competition from adjacent rows. Fewer rows of each generation per replication and an increased number of replications and locations were recommended for future research.

Lack of dominance or partial dominance for fewer days to silking was observed. The number of genes controlling days to silking varied from one to 23. Heritability estimates averaged 0.476 and ranged from 0.0 to 1.0. Epistasis for early silking was indicated in some crosses.

Independent gene systems for ear number and days to silking were indicated by low, non-significant genetic and simple correlations. In certain of the crosses studied, simultaneous selection for early-silking plants bearing two or more ears should lead to the isolation of early-silking, two-eared inbred lines for use in the northern Corn Belt.

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To my wife, Dottie, goes sincere thanks for her assistance and encouragement.

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INHERITANCE OF PROLIFICACY AND MATURITY IN CROSSES OF SOUTHERN x NORTHERN MAIZE GERM PLASM

INTRODUCTION

Recent interest in the development of hybrids which consistently produce two-eared plants has resulted from attempts to increase yields with one-eared hybrids at higher plant populations. Some hybrids in current use fail to respond in yield with increases in plant population due to the increased incidence of barren plants. Hybrids differ in their ability to resist barrenness, with those having one or more parents with the two-eared tendency showing some resistance to barrenness under stress. Few inbreds or hybrids adapted to the northern Corn Belt exhibit the two-eared characteristic.

During much of corn breeding in the Corn Belt, selection has been against prolificacy and in favor of single-eared varieties. This selection against prolifics dates to the days of hand harvest and continued for some time with the advent of mechanical harvest. In the South, personal preferences and labor economics have not resulted in nearly as much selection against prolifics. Therefore, there are more good sources of prolific characteristics in southern inbreds, hybrids, and open-pollinated varieties.

This study was conducted to obtain information on inheritance of the two-eared characteristic and maturity in crosses of early maturing single-eared inbred lines from the northern Corn Belt with late-maturing prolific inbreds from the South.

REVIEW OF LITERATURE

A. EAR NUMBER

Morphology, Histology, and Reproduction

Normal corn plants possess an ear bud in the axil of each leaf below the apical or main ear bud. During the development of the plant the ear primordia are formed in the axils of the new leaves until the tassel starts to differentiate (Hershey, 1934; Bonnett, 1948). At this stage no additional primordia are formed and the last one laid down usually becomes the main ear (Hershey, 1934). The lower or secondary buds may undergo considerable development or may disintegrate. In Corn Belt varieties seldom do more than the first and second ear buds extend beyond the leaf sheath (Kiesselbach, 1949).

Inselberg (1956) concluded from a morphological study of ear shoot development in the Corn Belt single crosses (WF9 x C103) and (L317 x R4) that the potential number of ears per plant was uniform but that the ear buds which developed into mature ears began to grow at an increased rate compared to non-developing ear buds approximately one week before silking.

Sowell (1959) using the normal and dwarf versions of the inbred Hy at a plant population of 52,000 plants per acre, observed 5% barren plants in the dwarf and 62% in the normal

inbred. He explained the ability of the dwarf to resist barrenness as due to the lack of competition between ear development and vegetative elongation following fertilization. The dwarf version stopped vegetative growth at flowering and used the products of photosynthesis for ear development.

Geography

Single-eared plants have been preferred in the northern Corn Belt and selection against the two-eared characteristic continues. However, prolific varieties, which develop an ear at more than one node, have been widely grown in the southern United States. Freeman (1955) described the performance of prolific hybrids in the southern United States and concluded that prolific hybrids are better adapted to extreme fluctuations in fertility and plant population than single-eared hybrids.

Environmental Modification of Morphology

The highest percentage of two-eared plants in hybrids reported in the literature is 85 percent (Freeman, 1955; Bauman, 1959). Bauman (1960) in Georgia, found that date of planting greatly affected the expression of the two-eared characteristic.

Effect of Increased Plant Population on Ear Number

Comparisons of single-eared and prolific hybrids for yield under various levels of fertility, population, and moisture

have been made by workers in several states (Josephson, 1957; Gibson, 1957; Zuber and Grogan, 1956; Zuber et al., 1960; Bauman, 1960). With increased plant population, ear number was reduced in both single-eared and prolific types. Under stress conditions, single-eared hybrids produced barren plants but no barrenness was observed in the prolific hybrids.

Sass and Loffel (1959) correlated ear bud development with barrenness at two planting rates. No difference in development of first and second ear buds was apparent until 74 days after planting. The period between the 68th and 74th day was critical to ear differentiation and elongation of silks.

Experiments using Corn Belt material indicated that hybrids with the highest expression of the two-eared characteristic at low plant populations tended to resist barrenness at high populations (Lang, et al., 1956; Findlay, 1956).

Effect of Shading on Ear Number

Stinson and Moss (1960) studied the effect of reduced sunlight on the yield of eleven hybrids under conditions of high fertility and irrigation. The hybrids were grouped as tolerant and intolerant to thick planting. Shade reduced the yield of both groups. The intolerant group was reduced approximately twice the amount of the tolerant group. Barrenness increased in both groups in the shade; the intolerant group had six times more barren plants than the tolerant group. They concluded that hybrids differ in their ability

to utilize sunlight and that this was the basis for tolerance or intolerance to high plant population.

Correlation of Yield with Morphological Characters

Numerous cases of correlations of yield with various morphological characters are reported in the literature. The characters showing the highest correlations with yield are usually those which have been termed "components of yield". The primary components of grain yield in corn according to Leng (1953) are: (1) number of ears per plant, (2) kernel weight, (3) kernel row number and (4) number of kernels per row. The secondary components are: (1) weight of grain per ear and (2) number of kernels per ear. He studied the effect of heterosis and the degree of dominance of 92 different F1 hybrids and parental lines. The hybrids were lower in ear number, nearly identical in row number, about 8 percent higher in kernel weight and 42 percent greater in number of kernels per row than their respective "top parents".

Inheritance of Ear Number

The percentage of total yield from first and second ears of crosses between Mexican, Brazilian, and Corn Belt lines were reported by Griffing and Lindstrom (1954). They were interested in the use of "exotic" germ plasm and its effect on the combining ability of derived lines and on the modification of Corn Belt agronomic characteristics. They

concluded that it was possible to introduce "exotic" germ plasm into a line and to restrict the yield of the inbred and crosses to a predominately single-eared type.

Gene Number and Degree of Dominance

To the author's knowledge, no estimates of the number of genes affecting ear number have been reported. Partial to complete dominance was found for genes controlling ear number estimated from the F₂ generations of three prolific single crosses by Robinson, et al. (1949). Lindsey (1957), working with three Corn Belt open-pollinated varieties, found the degree of dominance for ear number to be in the partially dominant range. Gardner and Lonnquist (1959), working with the F₂ and F₈ generations of the single cross (M14 x 187-2) estimated partial dominance for genes controlling ear number.

Heritability Estimates

Low heritability values have been reported for the two-eared characteristic. Collier (1959), in Texas, obtained heritability estimates of 12.5 and 11.2 in the second and third cycle of recurrent selection using two open-pollinated varieties. Low heritability for ear number may be inferred from the parent-offspring correlations of $r = 0.20 \pm .08$ in 1926 and $r = 0.12 \pm .09$ in 1927 by Jenkins (1929). Robinson et al. (1949) working with the single crosses CI.21 x NC7, NC16 x NC18, and NC34 x NC45, reported heri-

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tability values of 32.8, 14.0 and 26.0 for the three hybrids respectively.

B. MATURITY

Early maturity is essential in hybrids for the northern Corn Belt. Different measures of maturity have been used including hardness of grain, browning of husks, days to silking, physiological maturity, and moisture at harvest.

Environmental and Genetic Factors affecting Maturity

Shaw and Thom (1951) separated the development of the corn plant into three periods: (1) planting to emergence, (2) emergence to tasseling, and (3) tasseling to silking. Environmental factors were responsible for variations between hybrids for the period from planting to silking which averaged 65 days with a range of 20 days for the years 1921 to 1945. Very early, medium, and late maturing hybrids held their relative position in days from planting to tasseling. The time between tasseling and silking was shortest for the hybrids adapted to the area. Thus, the interval from planting to silking was the most important in determining the time of maturity. In a further study, they found the period from silking to maturity was affected little by weather conditions. The period from maturity to safe cribbing moisture, however, was greatly dependent upon environmental conditions.

Jones (1952) found genetic differences in days to silking and also from silking to physiological maturity. Some

inbred lines are late in silking but reach physiological maturity rapidly. Days from planting to silking would appear to be the logical basis for the corn breeder to adjust genetically as well as the period from silking to maturity. Dessureaux and Neal (1948) also found that, in general, hybrids that flower early also mature more quickly than late flowering types.

Inheritance: Dominance Relationships, Gene Numbers and Heritability Estimates

Emerson and East (1913) investigated the inheritance of days to flowering in crosses of the early flowering Tom Thumb popcorn variety and a late flowering Missouri variety. The F₁ was intermediate with wide segregation in the F₂ ranging beyond the means of the parents. Lindstrom (1943) reported dominance for early flowering in four crosses of corn inbreds.

Leng's (1951) report of heterotic effects in a single-cross for days from tassel initiation to anthesis were interpreted as indicating dominant gene action.

Yang (1949), using inbreds of similar maturity found the F₁ to be earlier in silking date than the earlier parent. He concluded that two or three independently inherited genes, with dominance for early silking, differentiated the two parents. Jones (1952) observed complete dominance of genes for early date of silking in six different crosses of early x late inbreds. Epistatic effects for the dominant early

genes from the inbred R53 were apparent. Gene number estimates varied from 5 to 19. Estimates of heritability for days to silking ranged from 11 to 48 percent with a mean of 29 percent.

Dominance of three major genes for early silking was reported by Mohamed (1959) using inbreds adapted to Egypt. Giesbrecht (1959) estimated that 3 to 7 genes with partial dominance and epistasis for earliness differentiated the cross of a very early Canadian inbred, V3, and the later maturing inbred B14. The heritability values obtained (59 percent in 1954 and 75.9 percent in 1955) indicated that selection within the segregating generations of the cross should be effective in isolating early maturing lines.

Giesbrecht cited estimates of gene numbers for date of silking from Zoebish (1950) who reported at least six factors, Agble (1954) who reported four factor pairs, and Bianchi and Miliani (1954) who estimated at least three and possibly four or five factors exhibiting dominance for early date of silking.

C. BIOMETRICAL CONSIDERATIONS

Although based on the principle of particulate genes discovered and elaborated by Mendel, characteristics controlled by several genetic factors seldom segregate into discrete phenotypic classes so that simple Mendelian ratios can be deduced. The continuous distribution of phenotypes is a result of the segregation of the underlying genetic

factors plus the masking effects of environment, the interaction of genes with each other and the interaction of the genetic factors with the environment. Among the significant contributions to the analysis of complex traits cited by Wright (1952) and Powers (1955) are: (1) Nilsson-Ehle's demonstration of the particulate nature of genetic factors controlling seed color in wheat, (2) Johannsen's evidence of the joint effects of genotype and environment on the phenotype, and (3) East's and his students' proof that a combination of genetic and environmental variations could produce the continuous variation of quantitative characters and that quantitative characters were indeed inherited according to the principles of Mendel.

The statistical procedures for the separation of total variance into genetic and environmental components are primarily due to Fisher and Wright. Other noteworthy contributions have been made by Mather (1949); Powers (1955); Lush (1943); Comstock and Robinson (1948); Lerner (1958) and Warner (1952).

The analysis of quantitative characters necessitates the use of (1) an adequate genetic design and (2) an adequate experimental design. A genetic design utilizing both segregating and non-segregating generations is essential for the estimation of environmental and genotypic variances. An experimental design which facilitates the analysis is one which minimizes or provides sufficient estimates of the genotype x environment variance and reduces the standard errors.

A knowledge of the number of genes, the degree of dominance, the type of gene action, and heritability allows the plant breeder to predict the results of various breeding schemes, probable rates of change, and to choose the most efficient procedures.

Genotype x Environment Interaction

The importance of considering the genotype x environment interactions in genetic investigations has been stressed by various writers (Sentz, 1954, and Comstock, 1955). The mistaking of variance due to genotype x environmental interaction as usable genotypic variance can lead to false conclusions and wasted effort. Collier (1959) and others, have suggested the use of the mean performance of several locations in an attempt to minimize the obscuring effects of genotype x environmental interactions upon selection and estimates of heritability. Heritability estimates based on one population at one location in one year are of doubtful value at least for certain traits. The need is apparent for a generalized estimate of heritability.

Tests of Scale - Transformations

In order to facilitate the analysis of quantitative characters an appropriate scale is essential.

The first step in an analysis of a quantitative character is a test for a scale on which the effects of the genes concerned are additive. Tests for adequacy of

scale and the limitations of these scales were discussed by Mather (1949), Powers (1941, 1950) and Falconer (1960). A satisfactory scale is one on which the action of the genes and non-heritable factors is additive on the average and one which removes the epistatic effects and allows dominance to take its own value on the scale used. Many types of transformations are available (Bartlett, 1947). As Falconer points out, transformations should not be made without good reason. For the first purpose of experimental observation is a description of the genetic properties of the population, and a scale transformation obscures rather than illuminates the description.

Partitioning of Variance

After an adequate scale has been found partitioning of the variance into genetic and non-genetic components follows. If the genotype x environment interaction is negligible, satisfactory separation of non-genetic variance from the total variance of the segregating populations can be accomplished as illustrated by Mather (1949). The estimation of the environmental variance from the mean variance of the parents or by the use of the F₁ variance may be of doubtful value due to the lack of competition between individual plants within the rows of the inbred parents plus the fact that the parents may differ considerably in maturity and be subjected to different climatic conditions at critical stages in their development (Sentz, 1954). The buffering effects

of heterozygosity in the F1 may restrict its value as an estimator of environmental variance. To circumvent this difficulty, Warner (1952) suggested the use of the segregating generations, F2 and first backcrosses, to estimate the additive genetic portion in estimating heritability. Warner's method assumes that the non-heritable components of variance are equal in the F2 and backcross populations. Burton (1951) used the variance of the F2 minus the variance of the F1 divided by the variance of the F2 as an estimate of maximum heritability. Lush (1943) called this "heritability in the broad sense". This estimate includes both the additive and the non-additive genetic variances. The formulae of Mather and Warner each estimate heritability in the "narrow sense" in which heritability is the ratio of additive genetic variance to the total phenotypic variance. Culp (1960) used both of the above methods in estimating heritabilities in sesame and stated that if dominance and epistasis were not present both formulae should give estimates which agree closely.

MATERIALS AND METHODS

Four early maturing Corn Belt inbreds (W64A, Oh28, Oh51 and R53) and three late maturing Tennessee inbreds (T115, T434 and T490) were used to study inheritance of ear number and maturity. W64A is single-eared, Oh28 and Oh51 exhibit a two-eared tendency, and R53 is intermediate. The Tennessee white inbred T115 and the yellow inbreds T490 and T434 were chosen as parents on the basis of observations taken in a preliminary experiment where they exhibited a high percentage of two-eared plants.

The genetic notation employed in each of the nine crosses was as follows:

- P₁ - the Corn Belt inbred
- P₂ - the Tennessee inbred
- F₁ - the single cross of Corn Belt x Tenn. inbreds
- F₂ - the selfed progeny of the F₁
- B₁ - the first backcross of F₁ to P₁
- B₂ - the first backcross of F₁ to P₂

Crosses used were: Oh51 x T115, W64A x T115, R53 x T490, W64A x T490, Oh51 x T490, Oh28 x T490, R53 x T434, W64A x T434, and Oh51 x T434.

A split-plot design with crosses as the main plots and generations as subplots was used to obtain precise estimates of generation variances. Four rows of each generation were

used. The crosses were randomized within replications, the generations randomized within crosses with the exception that the inbred parents were planted side by side to minimize the environmental variance between them. Three replications of the crosses (W64A x T115) and (Oh51 x T115) were planted in field I and the other crosses were planted in four replications in field II of the Crops Farm, East Lansing.

Field I was planted on June 2 and field II was planted on May 19, 1960. Two seeds were hand planted in hills one foot apart and the plants were thinned in the seedling stage to one plant per hill. Rows were 36 inches apart which gave a plant population of approximately 14,500 plants per acre. Complete fertilizer was applied in the row and nitrogen was added at the second cultivation.

The growing season was relatively cool during June and July. Moisture stress was evident in mid-July. Adequate moisture was available during the balance of the growing season.

All data were taken on individual plants. Date of silking observations were made daily by tagging each plant when the main ear shoot exhibited silk one-half inch in length. Number of ears per plant was recorded at harvest by examination of each ear for one or more developed kernels. A notation was made to distinguish competitive from non-competitive plants. Plants visibly diseased or damaged were discarded.

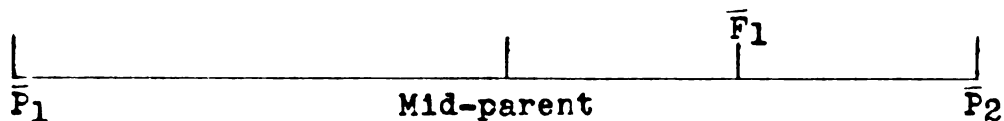
Date of silking was recorded only for the crosses (W64A x T115), (Oh51 x T115), (R53 x T490) and (W64A x T490). Silking dates were transformed to days from planting to silking. All plants were used in the analyses of variance of days to silking. Due to the effect of competition on ear number, data from competitive plants only were used in the analysis of variance of ear number.

The theoretical means and standard errors were calculated from formulae given by Powers (1955). A significant deviation of the F1 mean from the parental mid-point or average of the parents was interpreted as phenotypic dominance; however, it could be due to genetic epistasis (Figure 1). A non-significant difference between the mean of the F1 and the mean of one of the parents was considered to imply complete phenotypic dominance. A significant difference between the observed and theoretical F1 means and a significant difference between the observed F1 mean and the mean of the nearest parent was interpreted as partial phenotypic dominance. No significant difference between the observed F1 mean and the parental mid-point indicated no phenotypic dominance. Heterosis was implied whenever the mean of the F1 was significantly larger than the mean of the large parent or smaller than the mean of the small parent.

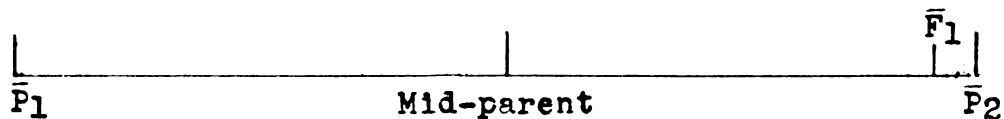
If there was no apparent phenotypic dominance exhibited by the F1 population, the mean of the F2 population should be equal to the mean of the F1 population and the means of the first backcross generations should agree closely with

Figure 1

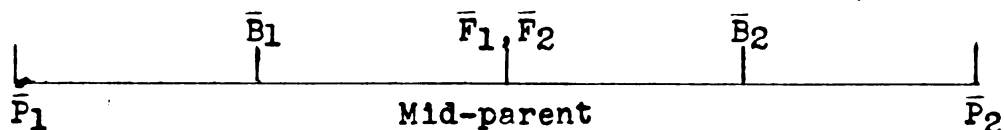
Graphic Illustrations of Dominance,
Epistasis, and Heterosis



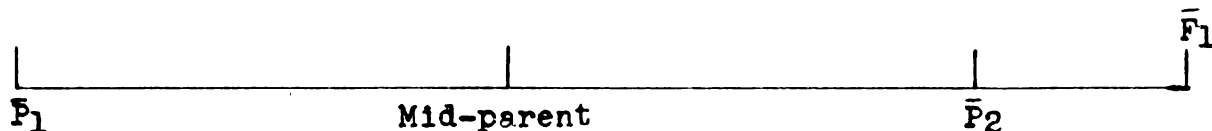
F_1 deviates significantly from mid-parent and also from the mean of the nearest parent - indicates partial phenotypic dominance or genetic epistasis. Epistasis in the broad sense includes many unseparable effects.



F_1 does not differ significantly from mean of one of the parents - indicates complete phenotypic dominance.



F_1 does not differ significantly from mid-parent indicating no phenotypic dominance. F_2 , B_1 , and B_2 do not differ from theoretical expected values indicating no genotypic dominance or epistasis.



F_1 deviates significantly above larger parent or below smaller parent - indicates heterosis.

their theoretical expected values. The backcross variances should be of similar magnitude also. However, if the F1 population displayed phenotypic dominance, the observed means of the segregating populations should not differ significantly from their theoretical expected means unless something other than allelic dominance was operating. The dominance deviations from simple additive gene action are considered in all of the formulae used to calculate the expected theoretical means; therefore, any significant difference between the theoretical and observed means of the segregating generations is due to non-allelic interaction or genetic epistasis.

With simple allelic dominance the mean of the F2 should fall between the parental mid-point and the F1 mean and the variance of the backcross to the dominant parent should be suppressed due to dominance and should be significantly smaller than the variance of the backcross to the recessive parent.

Deviations from the theoretical expected means and variances are considered to imply genetic epistasis or the interaction of non-alleles.

The formulae for the calculation of the theoretical means and their standard errors from Powers (1955) are as follows:

$$\text{Theoretical F1} = \frac{1}{2}(\bar{P}_1 + \bar{P}_2)$$

$$\text{Theoretical F2} = \frac{1}{4}(\bar{P}_1 + \bar{P}_2 + 2\bar{F}_1)$$

$$\text{Theoretical B1} = \frac{1}{2}(\bar{P}_1 + \bar{F}_1)$$

$$\text{Theoretical B2} = \frac{1}{2}(\bar{P}_2 + \bar{F}_1)$$

Standard error of theoretical $\overline{F_1} = \sqrt{\frac{SEP_1^2 + SEP_2^2}{4}}$

" " " " $\overline{F_2} = \sqrt{\frac{\frac{1}{2}(SEP_1)^2 + SE\overline{F_1}^2 + \frac{1}{2}(SEP_2)^2}{4}}$

" " " " $\overline{B_1} = \sqrt{\frac{SEP_1^2 + SE\overline{F_1}^2}{4}}$

" " " " $\overline{B_2} = \sqrt{\frac{SE\overline{F_1}^2 + SEP_2^2}{4}}$

EXPERIMENTAL RESULTS

Ear Number

To determine whether the heritable and non-heritable agents affecting ear number were acting in an additive manner, theoretical means were calculated for each segregating population using the arithmetic and logarithmic transformed data as suggested by Powers (1955). The observed and calculated arithmetic and geometric means and tests of significance are shown in Table 1. None of the F values indicated a significant difference between the observed means and the theoretical arithmetic or the logarithmic means. The test based on the F₂ population is the most sensitive because it includes a larger array of genotypes than either backcross population. If the genes and environmental agents are acting in an additive manner on the average, then the observed and theoretical arithmetic means should not differ significantly. If the effect of a gene substitution on the phenotypic expression of a character under consideration is not additive but multiplicative in action then the transformation of the observed data to logarithms is indicated. The non-significance of the F values obtained indicated that either scale would be satisfactory for the genetic analysis of the crosses.

TABLE 1

TESTS OF AGREEMENT BETWEEN OBSERVED AND CALCULATED
ARITHMETIC AND GEOMETRIC MEANS FOR EAR NUMBER

Cross	F2 Population			B1 to P1 Population			B1 to P2 Population		
	Ob- served Mean	Calculated Mean Arith- metrio	Geo- metrio	Ob- served Mean	Calculated Mean Arith- metrio	Geo- metrio	Ob- served Mean	Calculated Mean Arith- metrio	Geo- metrio
Oh51 x T115	1.91	2.04	1.95	1.88	1.80	1.72	2.30	2.29	2.21
W64A x T115	2.01	1.68	1.55	1.19	1.32	1.25	2.07	2.04	1.92
R53 x T490	1.42	1.57	1.48	1.39	1.48	1.38	1.67	1.66	1.59
W64A x T490	1.28	1.35	1.27	1.06	1.17	1.13	1.55	1.52	1.43
Oh51 x T490	1.82	1.68	1.61	1.70	1.64	1.56	1.89	1.73	1.66
Oh28 x T490	1.65	1.78	1.72	1.81	1.79	1.73	1.71	1.76	1.70
R53 x T434	1.54	1.88	1.77	1.25	1.69	1.60	1.49	2.08	1.96
W64A x T434	1.14	1.56	1.43	1.05	1.29	1.22	1.03	1.82	1.67
Oh51 x T434	1.82	1.79	1.71	1.74	1.70	1.64	1.80	1.87	1.78
Mean	1.62	1.70	1.61	1.45	1.54	1.47	1.72	1.86	1.77
F value	- -	1.16	0.02	- -	2.56	0.10	- -	1.72	0.21

To test individual crosses for adequacy of scale, Mather (1949) suggested the use of A, B, and C values. The values were calculated from the observed means as follows:

$$A = 2\bar{B}_1 - \bar{F}_1 - \bar{F}_1$$

$$B = 2\bar{B}_2 - \bar{P}_2 - \bar{F}_1$$

$$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$$

Significant values of A, B or C indicate that the scale is inadequate. These values and their standard errors calculated from arithmetic and logarithmic transformed data are presented in Table 2. In the crosses R53 x T434 and W64A x T434 the observed and logarithmic means are consistently closer to agreement than the observed and theoretical arithmetic means (Table 1), but the values of A, B and C in Table 2 indicated that the logarithmic transformation would not lead to improvement in scale. The arithmetic scale was used in the genetic analysis of ear number.

For each cross, population means and their standard errors, total and genetic variances are shown in Table 3. The genetic variances of the segregating populations were obtained by using the variance of the F1 populations as the estimate of environmental variance in all of the crosses except W64A x T490 and Oh28 x T490. The mean variances of the parents were used for these two crosses due to the unusually large variances of the F1 populations relative to the variances of the segregating populations. The Corn Belt inbred, Oh51, consistently developed a high percentage of two-eared plants. This consistency is shown by the over-all mean

TABLE 2
VALUES OF A, B, C AND THEIR STANDARD ERRORS

Cross	A \pm Std. Errors	B \pm Std. Errors	C \pm Std. Errors
<u>Arithmetic Values</u>			
Oh51 x T115	0.175 \pm 0.254	0.02 \pm 0.262	-0.533 \pm 0.334 **
W64A x T115	0.261 \pm 0.317	0.060 \pm 0.320	1.326 \pm 0.323 **
R53 x T490	-0.165 \pm 0.107	0.014 \pm 0.102	-0.621 \pm 0.318 **
W64A x T490	-0.229 \pm 0.040 **	0.048 \pm 0.101	-0.280 \pm 0.100 **
Oh51 x T490	0.124 \pm 0.078	0.311 \pm 0.096 **	0.540 \pm 0.428 **
Oh28 x T490	0.036 \pm 0.079	-0.110 \pm 0.094	-0.503 \pm 0.160 **
R53 x T434	-0.883 \pm 0.075 **	-1.17 \pm 0.098 **	-1.36 \pm 0.19 **
W64A x T434	-0.482 \pm 0.111 **	-1.58 \pm 0.83 **	-1.67 \pm 0.153 **
Oh51 x T434	0.072 \pm 0.087	0.135 \pm 0.110	0.140 \pm 0.176
<u>Logarithmic transformation values of A, B, C</u>			
Oh51 x T115	--	--	--
W64A x T115	1.812 \pm .0912**	.052 \pm .087	0.344 \pm .222
R53 x T490	0.048 \pm .030	.0008 \pm .03	-0.183 \pm .05 **
W64A x T490	-0.068 \pm .015 **	0.016 \pm 0.03	-0.082 \pm .051
Oh51 x T490	--	--	--
Oh28 x T490	0.072 \pm .023	0.041 \pm .028	0.157 \pm .049 **
R53 x T434	1.09 \pm 0.022	-0.291 \pm .025 **	-0.364 \pm .051 **
W64A x T434	-0.143 \pm .033 **	-0.430 \pm .027 **	-0.454 \pm .042 **
Oh51 x T434	--	--	--

TABLE 3

NUMBER OF PLANTS, MEANS AND THEIR STANDARD
ERRORS, TOTAL AND GENETIC VARIANCES FOR EAR NUMBER

Popu- lation	No. of plants	Mean ear number	S.E. of mean	Total variance	Genetic variance
<u>Oh51 x T115</u>					
P1	149	1.56	0.043	0.2687	- -
B1	137	1.88	0.038	0.1922	0.0768
F1	149	2.03	0.028	0.1154	- -
F2	123	1.91	0.056	0.3808	0.2654
B2	109	2.30	0.050	0.2693	0.1539
P2	96	2.55	0.076	0.5490	- -
<u>W64A x T115</u>					
P1	130	1.00	0.000	0.0000	- -
B1	111	1.19	0.036	0.1450	-0.0607
F1	111	1.64	0.043	0.2058	- -
F2	101	2.01	0.074	0.5525	0.3467
B2	89	2.07	0.037	0.1213	-0.0845
P2	46	2.44	0.098	0.4376	- -
<u>R53 x T490</u>					
P1	187	1.48	0.042	0.5740	- -
B1	148	1.39	0.046	0.5537	0.0652
F1	171	1.47	0.038	0.4915	- -
F2	205	1.42	0.034	0.4795	-0.0116
B2	119	1.67	0.045	0.4881	-0.0032
P2	146	1.86	0.030	0.3660	- -
<u>W64A x T490</u>					
P1	233	1.04	0.015	0.0501	- -
B1	235	1.06	0.018	0.0736	-0.0585
F1	213	1.30	0.032	0.2139	- -
F2	140	1.28	0.038	0.2069	0.0749
B2	148	1.55	0.043	0.2694	0.1373
P2	112	1.74	0.044	0.2140	- -

Table 3 continued

Popula- tion	No. of plants	Mean ear number	S. E. of mean	Total variance	Genetic variance
<u>Oh51 x T490</u>					
P1	187	1.57	0.034	0.2184	- -
B1	219	1.70	0.030	0.1978	-0.0212
F1	177	1.70	0.035	0.2191	- -
F2	33	1.82	0.105	0.3608	0.1417
B2	35	1.89	0.063	0.1404	-0.0787
P2	104	1.76	0.044	0.1981	- -
<u>Oh28 x T490</u>					
P1	64	1.91	0.040	0.1027	- -
B1	206	1.81	0.028	0.1655	0.0410
F1	136	1.67	0.038	0.1998	- -
F2	183	1.65	0.032	0.1837	0.0592
B2	148	1.71	0.036	0.1886	0.0641
P2	64	1.86	0.048	0.1462	- -
<u>R53 x T434</u>					
P1	249	1.39	0.029	0.2121	- -
B1	223	1.25	0.028	0.1769	0.0102
F1	112	2.00	0.039	0.1667	- -
F2	221	1.54	0.040	0.3557	0.1890
B2	260	1.49	0.033	0.2794	0.1127
P2	206	2.15	0.067	0.9276	- -
<u>W64A x T434</u>					
P1	215	1.09	0.025	0.1333	- -
B1	241	1.05	0.013	0.0434	-0.2442
F1	86	1.49	0.058	0.2876	- -
F2	250	1.14	0.022	0.1170	-0.1705
B2	228	1.03	0.010	0.0251	-0.2625
P2	195	2.15	0.058	0.6584	- -
<u>Oh51 x T434</u>					
P1	123	1.59	0.048	0.2876	- -
B1	185	1.74	0.033	0.2069	0.0519
F1	190	1.80	0.029	0.1550	- -
F2	145	1.82	0.038	0.2094	0.0544
B2	128	1.80	0.048	0.2960	0.1410
P2	180	1.94	0.046	0.3801	- -

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ear number of 1.57 ranging from a mean of 1.56 ears per plant in the Oh51 x T115 cross to a mean of 1.59 ears per plant in the Oh51 x T434 cross. The Tennessee inbred T115 possessed the strongest two-eared tendency of the inbreds used in this study. Every plant of the F1 population (Oh51 x T115) had three visible ear buds and developed two or more ears per plant. The relatively large variances shown in Table 3 for the inbred T115 may have been due in part to the late silking date with cool night temperatures and scarcity of pollen.

Dominance Relationships

A summary of the dominance relationships for ear number is shown in Table 4. The parents in the cross Oh51 x T115 represented the most prolific inbreds of each group. The Tennessee inbred T115 is very late in maturity and unadapted to the northern Corn Belt. It operated under different environmental conditions than the adapted inbreds during anthesis which may explain the relatively high variance of this population. All of the other populations silked much earlier in the season. The F1 was intermediate in ear number with each plant bearing two or more ears consistently. No dominance and no epistasis was indicated from a study of the various generations.

When the least prolific Corn Belt line, W64A, was crossed with the most prolific Tennessee line, T115, no dominance or epistasis was observed. Complete phenotypic and genic dominance for the one ear condition was shown by the various

TABLE 4
SUMMARY OF DOMINANCE RELATIONSHIPS FOR EAR NUMBER

<u>Oh51 x T115</u>	<u>W64A x T115</u>
No phenotypic dominance	No phenotypic dominance
No genic dominance	No genic dominance
No epistasis	No epistasis
<u>R53 x T490</u>	<u>W64A x T490</u>
Complete phenotypic dominance for one ear	Incomplete phenotypic dominance for one ear
Complete genic dominance for one ear	Incomplete genic dominance for one ear
No epistasis	No epistasis
<u>Oh51 x T490</u>	<u>Oh28 x T490</u>
No phenotypic dominance	Complete phenotypic dominance plus extreme
No genic dominance	heterosis for one ear
No epistasis	Complete genic dominance for one ear
	Epistasis for one ear
<u>R53 x T434</u>	<u>W64A x T434</u>
Complete phenotypic dominance for two ears	Incomplete phenotypic dominance for one ear
Complete genic dominance for one ear	Incomplete genic dominance for one ear
Epistasis for one ear	Epistasis for one ear
	<u>Oh51 x T434</u>
	No phenotypic dominance
	No genic dominance
	No epistasis

generations of the cross R53 x T490. Partial or incomplete phenotypic and genic dominance and no epistasis for lower ear number was shown by the cross W64A x T490.

The cross Oh51 x T490 represents a prolific Corn Belt inbred and the least prolific southern inbred used in this study. No phenotypic or genic dominance was indicated.

The one cross involving the most prolific Corn Belt inbred, Oh28, and T490 showed that the parents were not significantly different in number of ears per plant. In fact, the Corn Belt line was higher in mean ear number than the southern inbred. Complete phenotypic and genic dominance plus extreme heterosis for lower ear number was evident in the F1 population. Complete genic dominance and epistasis for one ear were indicated by the segregating generations.

In the cross R53 x T434, both the arithmetic and logarithmic scales were shown to be inadequate. Complete phenotypic dominance for two ears was indicated by the F1 population. The segregating generations all indicated genic dominance and epistasis for one ear.

The cross of the strongly one-eared inbred, W64A, with the strongly two-eared inbred, T434, showed incomplete dominance for lower ear number in the F1 population and incomplete genic dominance and epistasis for lower ear number in the segregating generations.

No phenotypic or genic dominance and no epistasis was indicated by the various populations of the cross Oh51 x T434.

Gene Number and Heritability

The estimates of the number of effective factors differentiating the parents of each cross and the heritability values are shown in Table 5. The Castle-Wright formula is as follows:

$$n = \frac{(\bar{P}_2 - \bar{P}_1)^2}{8(VF_2 - VF_1)}$$

The formula used by Burton (1951) from Wright is:

$$n = \frac{.25(.75 - h + h^2)D^2}{VF_2 - VF_1}$$

Where $h = \frac{F_1 - P_1}{P_2 - P_1}$

$$D = P_2 - P_1$$

P_1 - the mean of the smallest parent

P_2 " " " " largest parent

F_1 " " " " F_1 population

F_2 " " " " F_2 population

VF_1 the variance of the F_1 population

VF_2 " " " " F_2 "

The formulae estimate the number of effective factors governing the expression of a particular characteristic if the following assumptions apply:

- (1) No linkage between pertinent genes.
- (2) One parent supplies only plus factors and the other parent only minus factors among those in which they differ.

TABLE 5
GENE NUMBER AND HERITABILITY VALUES FOR EAR NUMBER

Cross	Gene Number		Heritability	
	Castle- Wright	Burton- Wright	Lush	Warner
Oh51 x T115	1.0	1.0	0.697	0.788
W64A x T115	1.0	1.0	0.628	1.000
R53 x T490	2.0	3.0	0.034	0.000
W64A x T490	1.0	1.0	0.362	0.343
Oh51 x T490	1.0	1.0	0.423	1.000
Oh28 x T490	1.0	1.0	0.322	0.073
R53 x T434	1.0	1.0	0.531	0.746
W64A x T434	2.0	2.0	0.000	0.000
Oh51 x T434	1.0	1.0	0.260	0.000

- (3) All genes are equally important.
- (4) No interaction exists between pertinent non-allelic genes.

If any of the above assumptions fail to apply, the estimates are incorrect and the actual number of genes is larger than the estimate indicates. Therefore, gene number estimates are to be considered as minimum gene numbers.

Two formulae were used to obtain the estimates of heritability. The first from Lush (1943) estimates heritability in the broad sense meaning that both additive and non-additive genetic variances are considered as heritable. The estimates of heritability obtained from the use of this formula are to be considered as maximum estimates of the heritabilities. The formula is as follows:

$$h^2 \text{ (heritability)} = \frac{VF_2 - VF_1}{VF_2}$$

The second formula from Warner (1952) estimates heritability in the narrow sense in that it uses the ratio of additive genetic variance to total phenotypic variance as the estimate of heritability. The formula is:

$$h^2 = \frac{2(VF_2) - (VBC_1 + VBC_2)}{VF_2}$$

The gene number estimates are quite low. The heritability values vary in magnitude from zero to 1.0 depending upon the particular cross and method of computation.

Correlations

Simple and genetic correlations of ear number with silking date for the crosses Oh51 x T115, W64A x T115, R53 x T490 and W64A x T490 are shown in Table 6. Silking data were not taken on the other crosses.

The genetic correlations were obtained by the use of the following formula used by Burton (1951) from Comstock:

$$\text{Genetic correlation} = \frac{CVXYF_2 - CVXYF_1}{\sqrt{(VXF_2 - VXF_1)(VYF_2 - VYF_1)}}$$

where CV = covariance and V = variance.

This formula attempts to remove the environmental variance and to estimate the degree of association of the gene system for ear number and the gene system for days to silking. The correlations are quite low indicating that genes for date of silking had little or no influence upon ear number.

Significant negative correlations for the F1 populations of Oh51 x T115 and W64A x T115 which were planted later and in a separate field from the other crosses indicate that the earlier silking plants developed more second ears than the later silking plants. However, only four to sixteen percent of the variability in silking date was associated with the variability in ear number in the three populations giving a significant correlation.

The genetic correlations for the crosses R53 x T490 and W64A x T490 are not valid due to the large variances of the F1 population compared with the variances of the F2 population.

TABLE 6
CORRELATIONS OF EAR NUMBER WITH SILKING DATES

Population	r	Genetic Correlation
<u>Oh51 x T115</u>		
F1	-0.219**	0.102
F2	0.100	
B1	-0.412**	
B2	-0.176	
<u>W64A x T115</u>		
F1	-0.284**	0.088
F2	0.012	
B1	0.009	
B2	0.064	
<u>R53 x T490</u>		
F1	0.194**	1.600
F2	0.112	
B1	0.137 *	
B2	0.104	
<u>W64A x T490</u>		
F1	0.007	2.247
F2	0.190**	
B1	0.141 *	
B2	-0.031	

** Significant at the 1% level
* Significant at the 5% level

Date of Silking

Tests for adequacy of scale included the analysis of variance of the observed population means and the theoretical arithmetic and geometric means. The F values showed significant differences between the observed and arithmetic theoretical means for the F2 and B2 populations (Table 7). The F values for the B2 populations were both significant but the value for the geometric means was considerably smaller than for the arithmetic means. Thus, a transformation to logarithms was indicated.

Mather's A, B, and C values (Table 8) indicated that the geometric means for the cross Oh51 x T115 were closer to the observed means than were the arithmetic means, thus, the logarithmic transformation was used in the genetic analysis of this cross. The other crosses indicated that neither the arithmetic nor geometric scale was adequate. The t values were considerably smaller for the arithmetic means and they were used for these three crosses. Different scales may be justified here owing to the fact that two fields and two planting dates were involved.

For days to silking, the means with their standard errors, total variances, and genetic variances are shown in Table 9. The earliest Corn Belt inbred used was R53 followed by W64A and Oh51. The two prolific inbreds T115 and T490 required approximately the same number of days to silk. The relatively large total variance of the inbred T115 in the cross W64A x T115 may be due in part to the later date of planting and to the cool night temperatures during the silking period.

TABLE 7

TESTS OF AGREEMENT BETWEEN OBSERVED AND CALCULATED ARITHMETIC AND GEOMETRIC MEANS FOR NUMBER OF DAYS FROM PLANTING TO SILKING

Cross	Observed mean	Calculated Mean	
		Arithmetic	Geometric
<u>F2 Population</u>			
Oh51 x T115	95.76	96.56	96.03
W64A x T115	93.80	96.50	95.67
R53 x T490	78.18	79.75	78.23
W64A x T490	81.38	83.20	82.53
Mean	87.28	89.00	88.12
F value	- -	18.44*	3.94
<u>B1 Population</u>			
Oh51 x T115	91.98	91.98	91.71
W64A x T115	87.71	90.62	89.95
R53 x T490	74.76	73.99	73.92
W64A x T490	77.77	78.48	78.44
Mean	83.06	83.77	83.50
F value	- -	1.36	0.45
<u>B2 Population</u>			
Oh51 x T115	98.93	101.24	100.56
W64A x T115	100.42	102.37	101.75
R53 x T490	83.84	85.54	84.72
W64A x T490	85.93	87.92	86.84
Mean	92.28	94.27	93.47
F value	- -	239.39**	21.20*

** Significant at the 1% level

* Significant at the 5% level

1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16
17	18	19	20
21	22	23	24
25	26	27	28
29	30	31	32
33	34	35	36
37	38	39	40
41	42	43	44
45	46	47	48
49	50	51	52
53	54	55	56
57	58	59	60
61	62	63	64
65	66	67	68
69	70	71	72
73	74	75	76
77	78	79	80
81	82	83	84
85	86	87	88
89	90	91	92
93	94	95	96
97	98	99	100

TABLE 8

VALUES OF A, B, C AND THEIR STANDARD ERRORS FOR DATE OF SILKING

Cross	A \pm Std. Errors	B \pm Std. Errors	C \pm Std. Errors
<u>Arithmetic Values</u>			
Oh51 x T115	0.20 \pm 1.06	-4.62 \pm 0.858**	-3.20 \pm 7.57
W64A x T115	-0.583 \pm 0.859	-3.90 \pm 0.852**	-10.88 \pm 1.72**
R53 x T490	1.55 \pm 0.523**	-3.36 \pm 0.550**	-6.29 \pm 0.567**
W64A x T490	-1.42 \pm 0.345**	-3.98 \pm 0.583**	-7.25 \pm 1.05**
<u>Logarithmic Scale</u>			
Oh51 x T115	0.00204 \pm 0.02	0.01486 \pm 0.015	-0.05958 \pm 0.071
W64A x T115	-0.02296 \pm 0.001**	-0.01190 \pm 0.00088**	-0.03590 \pm 0.0015**
R53 x T490	0.00970 \pm 0.0082	-0.01020 \pm 0.00091**	-0.02270 \pm 0.00052**
W64A x T490	-0.00780 \pm 0.0005**	-0.01030 \pm 0.00160**	-7.6665 \pm 0.00186 **

** Significant at the 1% level

TABLE 9

MEANS AND THEIR STANDARD ERRORS, TOTAL VARIANCES,
AND GENETIC VARIANCES FOR DAYS TO SILKING

Population	Mean-days to silking	S.E. of mean	Total variance	Genetic variance
<u>Oh51 x T115 (Logarithmic values)</u>				
P1	1.9647	0.01316	0.025812	- -
B1	1.9634	0.0013	0.000222	-0.000108
F1	1.9601	0.0149	0.000330	- -
F2	1.9675	0.0157	0.028821	0.028491
B2	1.9950	0.0014	0.000222	-0.000108
P2	2.0448	0.00165	0.000264	- -
<u>W64A x T115 (Arithmetic values)</u>				
P1	89.54	0.2074	7.0105	- -
B1	87.71	0.8783	16.6686	13.6975
F1	91.71	0.1436	2.9714	- -
F2	93.80	0.3390	15.8617	12.8902
B2	100.42	0.2605	8.7562	5.7848
P2	113.03	0.4625	21.1812	- -
<u>R53 x T490 (Arithmetic values)</u>				
P1	73.46	0.1144	3.4549	- -
B1	74.76	0.2361	13.1544	6.5521
F1	74.52	0.1645	6.6023	- -
F2	78.18	0.2121	10.6696	4.0673
B2	83.84	0.2704	13.0104	6.4081
P2	96.52	0.2006	7.2434	- -
<u>W64A x T490 (Arithmetic values)</u>				
P1	77.17	0.1175	3.8080	- -
B1	77.77	0.1363	5.0895	-2.1164
F1	79.78	0.1628	7.2059	- -
F2	81.38	0.2421	12.0714	4.86551
B2	85.93	0.2583	12.9480	5.7422
P2	96.05	0.2027	6.4111	- -

Dominance Relationships

A summary of the dominance relationships for days to silking is shown in Table 10. The various populations of the cross Oh51 x T115 exhibited no phenotypic dominance, no genic dominance, and no epistasis when the logarithmic transformed data were used for the analysis.

The crosses W64A x T115 and R53 x T490 exhibited incomplete phenotypic and incomplete genic dominance and possible epistasis for early silking. Incomplete phenotypic and genic dominance and no epistasis was indicated for the cross W64A x T490.

Gene Number and Heritability

Table 11 shows the estimates of gene numbers and heritabilities for silking date. The cross Oh51 x T115 gave rather low estimates for the number of effective factors differentiating the two parental inbreds.

The cross W64A x T115 indicated a one-to-five factor difference between the parents for silking date. The heritability estimates for this cross varied with the method of calculation used. The crosses R53 x T490 and W64A x T490 gave higher gene number and lower heritability estimates.

TABLE 10

SUMMARY OF DOMINANCE RELATIONSHIPS FOR DAYS TO SILKING

Oh51 x T115

No phenotypic dominance
No genic dominance
No epistasis

W64A x T115

Incomplete phenotypic dominance for early silking
Incomplete genic dominance for early silking
Possible epistasis for early silking

R53 x T490

Incomplete phenotypic dominance for early silking
Incomplete genic dominance for early silking
Possible epistasis for early silking

W64A x T490

Incomplete phenotypic dominance for early silking
Incomplete genic dominance for early silking
No epistasis

TABLE 11
ESTIMATES OF GENE NUMBER AND HERITABILITY FOR DAYS TO SILK

Cross	Number of Genes		Heritability Estimates	
	Castle-Wright	Burton-Wright	Lush	Warner
Oh51 x T115	1.0	1.0	0.989	1.000
W64A x T115	5.0	1.0	0.813	0.397
R53 x T490	16.0	23.0	0.361	0.000
W64A x T490	9.0	12.0	0.403	0.506

METHODS OF ESTIMATING GENERATION VARIANCES

The use of individual plant data to estimate generation variances is expensive. An alternative method using row means might allow the investigator to reduce the time and money required.

The use of individual plant data makes possible the separation of within-row environmental variance from the genetic variance among individuals of the same generation whereas the variance estimates obtained using row means combines the within-row environmental variance and the genetic variance.

If the within-row environmental variance for the characteristic under study is small relative to the genetic variance among individual plants of the same generation, then the use of row means for the calculation of generation variances may be suitable for genetic analysis. To obtain information regarding the amount of environmental variation one needs to observe the variation of the non-segregating generations. If the variances of the parental inbreds and the F₁ generation are low relative to the variances of the segregating generations the row mean method may be preferred to the individual plant method.

To compare the two methods an analysis of variance was made to obtain the between-row means within generation variances

and they are shown in Table 12 for ear number and Table 13 for date of silking. The magnitude of the variances calculated from the row means was lowered consistently compared with the variances obtained using individual plants. Several changes in the relative size of the variance of the F1 and F2 generations were obtained. In some cases the low number of plants was undoubtedly responsible for the unusually large change in variance. This is shown in the increased variances of the F2 and B2 populations of the cross Oh51 x T490. Changes in the relative size of the backcross variances are shown for the crosses W64A x T115, R53 x T490, Oh28 x T490, R53 x T434 for ear number and for the crosses Oh51 x T115 and W64A x T115 for days to silking. These changes in the relative size of the variances would greatly change the genetic analysis of these crosses. The use of the average of the parental variances as an estimator of the environmental variance in this study is of doubtful value due to the differences in maturity between the Corn Belt and Tennessee inbreds. The best estimate of environmental variances would be the F1 generations; therefore, any change in the variance of the F1 generation greatly affects the interpretation of the genetic situation.

TABLE 12
A COMPARISON OF METHODS OF ESTIMATING
GENERATION VARIANCES FOR EAR NUMBER

	Between plants within generations	Between row means within generations
<u>Cross #1 (Oh51 x T115)</u>		
P1	0.26870	0.00107
P2	0.54904	0.01657
F1	0.11540	0.00108
F2	0.38081	0.00393
B1	0.19224	0.00138
B2	0.26927	0.00176
<u>Cross #2 (W64A x T115)</u>		
P1	0.00000	0.00000
P2	0.43765	0.25398
F1	0.20575	0.00318
F2	0.55247	0.00530
B1	0.14505	0.00264
B2	0.12126	0.00573
<u>Cross #3 (R53 x T490)</u>		
P1	0.5740	0.00662
P2	0.3660	0.00485
F1	0.4915	0.01393
F2	0.4795	0.00352
B1	0.5537	0.00070
B2	0.4881	0.00439
<u>Cross #4 (W64A x T490)</u>		
P1	0.05014	0.00022
P2	0.21400	0.00591
F1	0.21386	0.00139
F2	0.20694	0.00208
B1	0.07361	0.00038
B2	0.26939	0.00574

Table 12 continued

	Between plants within generations	Between row means within generations
<u>Cross #5 (Oh51 x T490)</u>		
P1	0.21843	0.00111
P2	0.19814	0.00286
F1	0.21909	0.00152
F2	0.36076	0.15190
B1	0.19784	0.00140
B2	0.14037	0.09981
<u>Cross #6 (Oh28 x T490)</u>		
P1	0.10271	0.03566
P2	0.14625	0.00103
F1	0.19983	0.09948
F2	0.18371	0.00455
B1	0.16547	0.00118
B2	0.18856	0.00400
<u>Cross #7 (R53 x T434)</u>		
P1	0.21214	0.00414
P2	0.92763	0.00675
F1	0.16667	0.00000
F2	0.35571	0.00316
B1	0.17686	0.00266
B2	0.27938	0.00246
<u>Cross #8 (W64A x T434)</u>		
P1	0.13327	0.00198
P2	0.65844	0.00642
F1	0.28757	0.00016
F2	0.11705	0.00878
B1	0.04342	0.00041
B2	0.02509	0.00016
<u>Cross #9 (Oh51 x T434)</u>		
P1	0.28757	0.00472
P2	0.38006	0.01162
F1	0.15500	0.00093
F2	0.20938	0.00293
B1	0.20686	0.00141
B2	0.29598	0.02644

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TABLE 13
A COMPARISON OF METHODS OF ESTIMATING
GENERATION VARIANCES FOR DAYS TO SILKING

	Between plants within generations	Between row means within generations
<u>Cross #1 (Oh51 x T115)</u>		
P1	61.71226	0.46124
P2	17.47857	0.61043
F1	2.38825	0.05960
F2	337.59267	2.87455
B1	9.75320	0.16371
B2	13.67320	0.08125
<u>Cross #2 (W64A x T115)</u>		
P1	7.01053	0.06741
P2	21.18115	0.17110
F1	2.97144	0.05764
F2	15.86167	0.07840
B1	16.66859	0.15396
B2	8.75624	0.48923
<u>Cross #3 (R53 x T 490)</u>		
P1	3.45492	0.01258
P2	7.24335	0.17938
F1	6.60232	0.28314
F2	10.66959	0.02145
B1	13.15441	0.08344
B2	13.01043	0.11697
<u>Cross #4 (W64A x T490)</u>		
P1	3.80800	0.04312
P2	6.41110	0.06667
F1	7.20586	0.01642
F2	12.07137	0.10493
B1	5.08946	0.04129
B2	12.94803	0.16643

Expected Genetic Gain

The formula used for calculating the expected genetic gain from selection was as follows:

$$\Delta G = i h^2$$

$$i \text{ (selection intensity)} = \frac{Z - v}{v} \times \sigma$$

Z = the ordinate of the normal curve area
at the point of truncation

v = the percent of the population saved
for breeding

σ = the generation standard deviation

For the simultaneous selection of two traits the formula is modified as follows:

$$i = \frac{Z - \sqrt{v}}{\sqrt{v}} \times \sigma$$

The expected genetic gain from simultaneous selection of five percent of the earliest silking, two-eared plants in the F2 population of the various crosses are shown in Table 14. The expected genetic gain from selection of the earliest silking, five percent of the plants in the F2 generation of the four crosses for which silking data were available are shown in Table 15. Similar calculations for ear number are shown in Table 16. Undoubtedly the realized gains in ear number will be somewhat lower than the predicted gains because of the expected year-to-year variation in the heritability values used in the calculations.

TABLE 14

EXPECTED GENETIC GAIN FROM SIMULTANEOUS SELECTION OF THE
EARLIEST-SILKING, TWO-EARED PLANTS IN THE F2 POPULATIONS
WITH FIVE PERCENT OF THE POPULATION SELECTED

Cross	Expected Genetic Gain	
	Ear Number	Days to Silking
Oh51 x T115	0.65003	2.4556
W64A x T115	0.99361	2.11375
R53 x T490	0.00000	0.00000
W64A x T490	0.20858	2.34982

TABLE 15

EXPECTED GENETIC GAIN FROM SELECTION OF THE FIVE
PERCENT EARLIEST SILKING PLANTS IN THE F2 POPULATION

Cross	Expected Genetic Gain for Days to Silking
Oh51 x T115	3.78789
W64A x T115	3.26054
R53 x T490	0.00000
W64A x T490	3.62467

TABLE 16

EXPECTED GENETIC GAIN FROM SELECTION OF FIVE PER-
CENT OF THE MOST PROLIFIC PLANTS IN THE F2 POPULATION

Cross	Expected Genetic Gain for Ear Number
Oh51 x T115	1.0027
W64A x T115	1.5327
R53 x T490	0.0000
W64A x T490	0.3217
Oh51 x T490	1.2384
Oh28 x T490	0.0645
R53 x T434	0.9176
W64A x T434	0.0000
Oh51 x T434	0.0000

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DISCUSSION

Previous research indicated that environmental factors were capable of modifying the phenotypic expression of the number of ears per plant. Therefore, the results of the scaling tests obtained in the various crosses of this study are to be expected and undoubtedly will be found in future work with the characteristic.

Crosses of the strongly two-eared Corn Belt inbred, Oh51, with the two-eared southern inbreds exhibited no phenotypic or genic dominance and no epistasis.

Crosses involving the predominately one-eared inbred, W64A, displayed incomplete or no phenotypic and genic dominance for one ear with evidence of epistasis for one ear in the cross with T434.

The inbred R53 was intermediate in ear number as a line and varied in its dominance reactions in crosses. A study of the population means of the cross R53 x T434 revealed non-additivity and strong gene interaction. The F1 mean clearly indicated phenotypic dominance for two ears, but all of the segregating population means indicated genic dominance and epistasis for the one ear condition. The genetic situation of this cross is not clear. One explanation for the lack of agreement between the F1 population and the segregating populations may be that the F1 plants may have been more vigorous

than those of the segregating generations and the genes for the two-eared condition in the F1 plants may have been able to express their effects phenotypically. The possibility of threshold effects where a basic number of equally important genes for the two-eared condition are necessary before any phenotypic effect can be produced and the addition of one or more genes are then capable of producing a strong phenotypic expression may be nullified in this case. The B2 population should possess more of the genes for two-ears than any of the other populations but the mean of the B2 was below the means of the F1 and F2 for ear number. The possibility remains, however, for a threshold gene number and a residual genotype which confers the necessary vigor for the strong expression of the two-eared condition in the F1 population.

The Corn Belt line with the strongest two-eared tendency, Oh28, when crossed to T490, the least prolific southern inbred used in this study, exhibited complete phenotypic dominance plus heterosis for lower ear number in the F1 population. Complete genic dominance and epistasis were displayed by the segregating generations.

Previous research has indicated that the two-eared characteristic was recessive in nature. Based on the findings of this study, no generalized statement regarding the dominance of the one-eared condition or the recessiveness of the two-eared condition can be made as shown in the lack of dominance in the cross of W64A x T115 which represents the least and the most prolific lines investigated. Depending upon the specific

cross, the dominance relationships varied from complete dominance for higher ear number to complete dominance for lower ear number. In general, dominance was in the direction of lower ear number. Previous research has indicated partial to complete dominance for lower ear number only.

Formulae for estimating the number of effective factors differentiating the parents apply only when one parent contributes plus factors and the other parent contributes minus factors and genetic and environmental agents have equal effects in all genotypes. Further, the factors must be additive in action with no dominance or linkage. The estimates of gene numbers obtained are minimum estimates and vary from actuality as the above conditions failed to be realized. In general, the estimates indicated few genes involved in the inheritance of ear number.

The formulae for the estimation of heritability are also based on the assumptions of no linkage of pertinent genes, additive gene action, equal effects of genes and no genotype-environmental interaction. In the broad sense heritability is the ratio of genetic variance to total phenotypic variance. In the narrow sense heritability is the ratio of additive genetic variance to the total variance. Since in an F₂ the additive variance is the only fixable variance, the estimate of heritability in the narrow sense is more valuable to the breeder for it provides a measurement of the effectiveness of selection. In the field, heritability is a measure of the reliability of the phenotype as an indicator of genotype. High

heritability estimates for ear number were obtained where the crosses had shown no dominance and no epistasis as in the cross of Oh51 x T115, and lower estimates were obtained where complete dominance and/or epistasis was indicated. The average heritability calculated from the variances of the F2, BC1 and BC2 populations was 0.439 with separate estimates ranging from 0.0 to 1.0. The average heritability for ear number reported by Robinson, et al. (1949) was 0.243. Values of 0.125 and 0.112 were reported by Collier (1959) and the squared correlation coefficients reported by Jenkins (1929) were 0.04 and 0.014. The calculated heritability values obtained in this study are much higher than previously reported values; however, the populations used in this study involved early and late maturing inbreds whereas the other investigators used populations of similar maturity and adaptation.

Dominance relationships for days to silking varied from no phenotypic and genic dominance in the cross Oh51 x T115 to incomplete phenotypic and genic dominance for early silking in the crosses W64A x T115, R53 x T490, and W64A x T490. Possible epistasis for early silking was indicated for the crosses W64A x T115 and R53 x T490. These findings are in agreement with previously reported research which covered a wide range of material and locations.

Calculated gene numbers varied from one to 23 in the present study. Previously reported gene numbers have indicated relatively few genes for days to silking. Heritability values using the Warner formula averaged 0.476 with a range of 0.0 to 1.0. Jones (1952) reported an average heritability

for days to silking of 0.290 ranging from 0.11 to 0.48 depending on the particular cross. Giesbrecht (1959) reported heritability values of 0.59 and 0.759 for the same cross in two consecutive years.

The segregating generations of the cross Oh51 x T115 exhibited no phenotypic and no genic dominance for early silking. The number of genes differentiating the parents was one for both ear number and days to silking. This situation, plus the low, non-significant genetic correlation between ear number and date of silking indicated that there were few genes involved and that they segregated and acted independently. The high heritability values obtained for each characteristic lead to the conclusion that rapid progress could be made by selection of early silking, two-eared plants in the segregating generations of this cross.

In the cross W64A x T115 relatively high heritability estimates were obtained for both ear number and days to silking. The gene number difference between the parents for date of silking ranged from one to five. Incomplete phenotypic and genic dominance plus possible epistasis for early silking was observed. Low, non-significant genetic correlations indicated independent gene systems for ear number and days to silking. The breeder could expect good progress in isolating early silking, two-eared inbreds from the segregating generations of this cross.

The cross R53 x T490 exhibited incomplete phenotypic and genic dominance of genes for early silking and possible

epistasis. The estimate of the number of genes involved in ear number - two to three - was the highest of the nine crosses used in this study. The low heritability estimates for date of silking make this cross of doubtful value in a breeding program.

The cross W64A x T490 exhibited incomplete phenotypic and genic dominance for one ear. Estimates of gene number difference between the parents were one (1) and the heritability values were moderate. This cross showed partial dominance for early silking controlled by nine to twelve genes. The relatively good heritability values indicate that fair progress could be made by selection in the segregating generations of this cross for early-silking, two-eared inbreds.

The remaining crosses were studied regarding ear number only. The cross W64A x T434 displayed incomplete phenotypic and genic dominance and epistasis for one ear. The estimate of gene number was two. The heritability estimates were the lowest obtained for any of the crosses due to the large variances of the non-segregating populations.

The F1 population of the cross R53 x T434 exhibited incomplete phenotypic dominance for two ears; however, the segregating generations displayed incomplete genic dominance and epistasis for lower ear number. Despite this evidence of non-additive gene action, the heritability estimates for this cross were relatively high indicating that good progress could be made from selection in the segregating populations.

Complete phenotypic dominance and heterosis for lower ear number was observed for the F1 of the cross Oh28 x T490 and

complete dominance and epistasis for lower ear number were displayed by the segregating generations. The estimate of gene number was one. The low heritability value indicated that poor progress would be made by selection in the segregating generations of this cross.

The F₁ of the cross Oh51 x T490 displayed no phenotypic dominance and the segregating generations exhibited no dominance or epistasis for ear number. The estimate of gene number was one and the heritability was one also. Rapid progress should be made from selection in the segregating generations of this cross.

No dominance or epistasis was observed in any population of the cross Oh51 x T434. The estimate of gene number was one. The variance of the F₂ population was relatively small compared with the variances of the B₁ and B₂ which resulted in a low estimate of heritability.

In general, it appears that relatively few genes control the two-eared characteristic and that environmental agents and competitive processes within the plant may influence the phenotypic expression of the characteristic.

A comparison of generation variance estimates obtained using individual plant variances versus row mean variances showed significant differences between the two methods. The use of individual plant data makes possible the separation of within-row environmental variance from the genetic variance among individuals of the same generation which is needed when investigating a characteristic as sensitive to environment

as the number of ears per plant, especially when using unadapted material.

Due to long term selection against the two-eared characteristic in the northern Corn Belt, present day corn breeders desiring to obtain early maturing, two-eared inbreds for use in hybrid combinations must use relatively unadapted two-eared breeding material.

Information regarding the inheritance of maturity and the two-eared characteristic in early x late crosses is essential to an efficient program where the goal of the breeder is the isolation and use of early maturing, two-eared inbreds.

Data from a specific number of competitive plants in each row should be used in future research to overcome any possible metrical bias introduced in adjusting the mean squares which is necessary when unequal numbers of plants per row are included. Every precaution should be used to obtain full plant populations.

The analysis of variance of crosses indicated no significant differences between the mean of the four rows per generation per replication used in this study; therefore, future experiments could use single rows of the inbred and F1 populations and two rows of the segregating populations.

The experiments should be planted early in well-drained soil to assure that the late silking inbred flowers before the cool nights of late summer which may interfere with normal flowering and seed set.

Future experiments should include several locations to increase the reliability of the estimates of heritability because of genotype x environment interaction.

Future research regarding the effect of date of planting should be conducted in the northern Corn Belt due to the effects of date of planting upon the expression of ear number reported by Bauman (1960).

As suggested by Jones (1952) the use of dominant, epistatic genes carried by some Corn Belt inbreds might enable the breeder to take advantage of factors for high yield of some later maturing inbreds. By using two early inbreds containing dominant, epistatic genes as one single cross parent and a later maturing single cross as the second parent, a double cross hybrid could be produced which could be early and high in yield. One disadvantage of the method would be that the parents would flower at different times necessitating two planting dates. Jones further suggested the production of a modified double cross hybrid using two first backcross generation populations in which an early silking inbred carrying dominant, epistatic genes for early silking would be used as the recurrent parent of each single cross with a high yielding later-silking inbred used as the non-recurrent parent.

The genetic correlations obtained indicated independent gene systems for ear number and maturity; therefore, simultaneous selection for early-silking plants bearing more than one ear should lead to the isolation of early silking, two-eared inbred lines. The low gene number estimates, and

relatively high heritability estimates for the crosses Oh51 x T115, W64A x T115 and W64A x T490 indicate that the desired progress could be made.

SUMMARY

Four early-maturing Corn Belt inbreds (W64A, Oh51, R53 and Oh28) and three late-maturing Tennessee inbreds (T115, T434 and T490) were used to study the inheritance of ear number and days to silking.

All data were taken on individual plants. Date of silking observations were made daily by tagging each plant when the main ear shoot exhibited silk one-half inch in length. Number of ears per plant was recorded at harvest by examination of each ear for one or more developed kernels.

Theoretical means and standard errors were calculated and tests were run for adequacy of scale. Gene numbers, dominance relationships and heritability values were calculated using the formulae available in the literature. Gene numbers varied from one to three for ear number. Dominance relationships varied from complete dominance for genes controlling the two-eared characteristic through no dominance to complete dominance for one ear.

Previous research had indicated that the two-eared characteristic was recessive in nature. This study showed that the dominance relationships varied depending upon the particular parents used.

Epistatic effects varied similarly. Heritability values varied from 0.0 to 1.0 averaging 0.439 which was higher than any previously reported estimate of heritability for the two-eared characteristic.

The inbred, Oh51, in crosses, showed no dominance and no epistasis. No generalized statement regarding the dominance of the one-eared condition can be made as shown by the lack of dominance in the cross W64A x T115 which represented the least and the most prolific lines investigated.

No significant difference between the means of the four rows of each generation per replication indicated that the effect of between-row competition, or lack of competition between the two outside rows of the generations, did not affect the expression of ear number. Thus, single rows of non-segregating generations and two rows of the segregating generations and the use of more replications and locations were proposed for future experiments. The use of several locations would give a more reliable estimate of genotype-environment interaction and more reliable estimates of heritability.

The fact that the F1 of the cross of Oh28 x T490, both of which possess a strong two-eared tendency as lines, showed complete phenotypic dominance and extreme heterosis for lower ear number indicates that the use of a two-eared tester may not be the best choice.

No dominance or incomplete dominance for fewer days to silking was observed in all crosses. Gene number estimates

for days to silking varied from one to 23. Heritability estimates averaged 0.476 and ranged from 0.0 to 1.0. The results obtained regarding days to silking are in agreement with previous work in which relatively few genes with some degree of dominance and epistatic effects for early silking were found.

Low, non-significant genetic and simple correlations between silking date and ear number indicated that two independent gene systems are involved. Simultaneous selection for early silking plants bearing more than one ear should lead to the isolation of early silking, two-eared inbred lines.

A comparison of generation variance estimates obtained using individual plant variances versus row mean variances showed considerable differences between the two methods.

LITERATURE CITED

- Agble, W. K. The Inheritance of Maturity as Measured by Time of Silking and other Character Associations in Zea Mays. PhD Thesis, Univ. of Minn., 1954.
- Bauman, L. F. Environmental Interactions with Prolific Hybrids. Proceedings of 14th annual Hybrid Corn-Industry-Research Conf. 1959.
- Bauman, L. F. Relative Yields of First (Apical) and Second Ears of Semi-Prolific Southern Corn Hybrids. Agron. J. 52:220-222 1960.
- Bartlett, M. S. The Use of Transformations. Biometrics 3:39-52 1947.
- Bianchi, A., and Milliani, I. Falter genetici nil tempo di ireitura in um increcio di zea mays Genet. Agrar. 4:68-90 (Plant Breeding Abstracts 24, p.554) 1954.
- Bonnett, O. T. Ear and Tassel Development in Maize. Miss. Bot. Gard. Ann. 35:269-287. 1948.
- Burton, G. W. Quantitative Inheritance in Pearl Millet Agron. Jour. 43:409-417 1951.
- Collier, J. W. Three cycles of reciprocal recurrent selection. Proceedings of 14th Annual Hybrid Corn Industry-Research Conf. pp. 12-23, 1959.
- Comstock, R. E. and H. F. Robinson. The Components of Genetic Variance in Populations of Biparental Progenies and Their Use in Estimating the Average Degree of Dominance. Biometrics 4:254-266. 1948
- Comstock, R. E. Theory of Quantitative Genetics; Synthesis. Cold Spring Harbor Symposia on Quantitative Biology. Vol. XX, 1955.
- Culp, T. W. Inheritance of Plant Height and Capsule length in Sesame, Sesamum Indicum L. Agron. J. 52:101-103. 1960.

- Dessureaux, L., Neal, N. P. and R. A. Brink. Maturation in Corn. J. Am. Soc. Agron. 40:733-745. 1948.
- Emerson, R. A., and East, E. M. The Inheritance of Quantitative characters in Maize. Neb. Agr. Exp. Sta. Res. Bul. No. 2, 1913.
- Falconer, D. S. Introduction to Quantitative Genetics The Ronald Press Company, New York. 1960.
- Findlay, Don E., Earl Leng and E. B. Earley. Effect of varied plant populations and thinning dates on ear and tiller development and on stover grain ratios in corn. Agron. Jour. 48:289. 1956.
- Freeman, W. H. Evaluating Hybrids in the South. Proceedings of 10th Hybrid Corn Industry-Research Conf. 1955.
- Gardner, C. O. and J. H. Lonnquist. Linkage and degree of dominance of genes controlling quantitative characters in maize. Agron. J. 51:524-528. 1959.
- Gibson, Robt. H. The influence of plant populations on the yield and other characteristics of corn. M.S. Thesis, Univ. of Tennessee. 1957.
- Giesbrecht, J. Corn Maturity Inheritance. Canadian J. Genetics Cyt. 1959:1:329-38. PhD Thesis, Univ. of Minn., 1959.
- Griffing, Bruce and Lindstrom, E. W. A Study of the Combining Abilities of Corn Inbreds having Varying Proportions of Corn Belt and Non-Corn Belt Germ Plasm. Agron. Jour. 46:545-552. 1954.
- Hershey, A. L. A Morphological Study of the Structure and Development of the Stem and Ears of Zea Mays. PhD Thesis, Iowa State College. 1934.
- Inselberg, Edgar. Factors Affecting Earshoot Development in Dent Corn. Diss. Abst. 16 (9) 1975 1956 Publication #18, 153.
- Jenkins, M. T. Correlation Studies with Inbred and Cross-bred strains of Maize. Jour. Agric. Res. 39:677-721 1929.
- Jones, Champ M. An Inheritance Study of Corn Maturity. PhD Thesis, Michigan State College. 1952.
- Josephson, L. M. Breeding for Early Prolific Hybrids. Proceedings Twelfth Hybrid Corn Industry-Research Conference 71-79. 1957.

- Kiesselbach, T. A. The Structure and Reproduction of Corn. A.E.S. Research Bul. No. 161., Univ. of Neb. College of Agric., November, 1949.
- Lang, A. L., J. W. Pendleton and G. H. Dungan. Influence of Population and Nitrogen Levels on Yield and Protein and Oil Content of Nine Corn Hybrids. Agron. Jour. 48:284-289. 1956.
- Leng, E. R. Time-Relationships in Tassel Development in Inbred and Hybrid Corn. Agron. Jour. 43:445-459. 1951.
- Leng, E. R. Expression of Heterosis and Apparent Degree of Dominance in the Major Components of Grain Yield in Maize. Genetics 38:674-675. 1953.
- Lerner, I. M. The Genetic Basis of Selection. John Wiley and Sons, Inc. New York. 1958.
- Lindsey, M. F. Genetic Variance Estimates in Three Corn Belt Varieties of Corn. M.S. Thesis, Univ. of Nebraska, January, 1957.
- Lindstrom, E. W. Experimental Data on the Problem of Quantitative Character Inheritance in Maize and Tomatoes. Genetics 28:81-82. 1943.
- Lush, J. L. Animal Breeding Plans. Iowa State Press, Ames Iowa. 1943.
- Mather, K. Biometrical Genetics. Dover Publications, 1949.
- Mohamed, Aly H. Inheritance of Quantitative Characters in Zea Mays. I. Estimation of the Number of Genes Controlling the Time of Maturity. Gen. 44:713-724. 1959.
- Powers, LeRoy and C. B. Lyon. Inheritance Studies on Duration of Developmental Stages in Crosses within the Genus Lycopersicon. J. Agr. Res. 63:129-148. 1941.
- Powers, LeRoy. Determining Scales and the Use of Transformations in Studies on Weight per Locule of Tomato Fruit. Biometrics 6: No. 2, 145-163 1950.
- Powers, LeRoy. Components of Variance Method and Partitioning Method of Genetic Analyses Applied to Weight per Fruit of Tomato Hybrid and Parental Populations. USDA Technical Bulletin No. 1131. 1955.
- Robinson, H. F., R. E. Comstock and P. H. Harvey. Estimates of Heritability and Degree of Dominance in Corn. Agron. Jour. 41:353-59. 1949.

- Sass, J. E. and F. A. Loeffel. Development of Axillary Buds in Maize in Relation to Barrenness. Agron. Jour. 51:484-86. 1959.
- Sentz, J. C., H. F. Robinson and R. E. Comstock. Relation between Heterozygosis and Performance in Maize. Agron. Jour. 46:514-520. 1954.
- Shaw, R. H. and H. C. S. Thom. On the Phenology of Corn, the Vegetative Period. Agron. Jour. 43:9-15. 1951.
- Shaw, R. H. and H. C. S. Thom. On the Phenology of Field Corn, Silking to Maturity. J. Am. Soc. Agron 43:541-546. 1951.
- Sowell, Walter Frank. Factors Contributing to the Superior Yielding Ability of Compact Semi-Dwarf Maize at High Population. PhD Thesis, Purdue University, 1959. Diss. Absts. Vol. XX, No. 7, January, 1960.
- Stinson, Harry T., Jr. and Dale N. Moss. Some Effects of Shade upon Corn Hybrids Tolerant and Intolerant of Dense Planting. Agron. Jour. 52:482-484. 1960.
- Warner, J. N. A Method of Estimating Heritability. Agron. Jour. 44:427-430. 1952.
- Wright, S. The Genetics of Quantitative Variability. Quantitative Inheritance, Agr. Res. Council, Edited by C. R. Reeve and C. H. Waddington. London, Her Majesty's Stationery Office, pages 5-41. 1952
- Yang, Y. Study on the Nature of Genes Controlling Hybrid Vigor, as it Affects Silking Time and Plant Height in Maize. Agron. Jour. 41:309-12. 1949.
- Zoebisch, O. C. The Inheritance of Some Quantitative Characters in Zea Mays. PhD Thesis, Univ. of Minn. Minneapolis, Minn. 1950.
- Zuber, M. S. and C. O. Grogan. Rate of Planting Studies with Corn. Missouri Agric. Exp. Sta. Bul. 610, 1956.
- Zuber, et al. Rate of Planting Studies with Prolific and Single-ear Corn Hybrids. Univ. of Missouri College of Agric. A.E.S. Res. Bulletin 737, Sept., 1960.

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